The Dissertation Committee for Naiara Sardinha-Pinto Certifies that this is the approved version of the following dissertation:

Consequences of Habitat Fragmentation: Connectivity Lies in the Eye of the Beholder

Committee:

Timothy H. Keitt, Supervisor

Mauro Galetti

Lawrence Gilbert

Mathew Leibold

Lauren Ancel Meyers

Rodrigo Sierra

Consequences of Habitat Fragmentation: Connectivity Lies in the Eye of the Beholder

by

Naiara Sardinha-Pinto, Bsc.

Dissertation

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Doctor of Philosophy

The University of Texas at Austin

May 2008

Dedication

To Cylon and Jennipher

Acknowledgements

I wish to acknowledge Sérgio Furtado, my undergraduate advisor who introduced me to the field of spatial ecology. I am most grateful to Tim Keitt and my committee for the patience and the encouragement you offered during the past six years. I would also like to thank the Brazilian government, particularly IBAMA. In denying me the opportunity to do field work in my own country, you encouraged me to find an excellent study site in Mexico. I would also like to thank all my colleagues from the Keitt lab. Last but not least, I am thankful to Trevon Fuller, someone I have the privilege to have as a husband, a friend, and a colleague.

Consequences of Habitat Fragmentation: Connectivity Lies in the Eye of the Beholder

Publication No._____

Naiara Sardinha-Pinto, Ph.D.

The University of Texas at Austin, 2008

Supervisor: Timothy H. Keitt

This dissertation was motivated by the problem of pattern and scale in ecology. All chapters present models that aim at predicting species' responses to habitat fragmentation. Chapters differ mainly in the nature of the responses being investigated: spatial variation in abundance, or dispersal. In each chapter, I illustrate how current models can be modified to incorporate species' perception of the landscape. Three sources of bias have been examined here: interspecific variation in (i) ecological neighborhood, (ii) ecological generalization, and (iii) in the response to regional processes. I have deliberately moved away from traditional single-scale, patch-based measures of landscape connectivity. Great emphasis has been placed on the anthropogenic aspect of the landscape, and on the role of the landscape matrix.

Habitat fragmentation is a common feature of most (if not all) biodiversity hotspots. I hope the tools shown here can serve as general approaches to study how species are differentially affected by habitat fragmentation, and to ultimately understand how disturbed landscapes can "filter" natural communities.

Table of Contents

List of Tables

List of Figures

Chapter 1: What is a patch? Reflections on measures of landscape pattern

PATTERN AND SCALE

Across all biological disciplines, the development of tools to better characterize pattern is critical to understanding process. In developmental biology, researchers investigate how patterns of tissue organization result from biochemical pathways and rates of gene expression. In evolutionary biology, the speciation process gives rise to the tree-like pattern representing historical relationships among organisms. Landscape ecology is defined as the study of the relation between pattern and process (Wiens et al. 1993). Still, progress needs to be made to operationalize the process of filtering relevant patterns. In this dissertation, I focus on patterns of landscape connectivity and fragmentation. I propose that traditional approaches to measure pattern are not always useful to infer process. Thus existing methods are modified in order to isolate patterns that are relevant for a particular organism given its natural history traits such as dispersal ability, habitat preferences, and foraging behavior.

The Theory of Island Biogeography (MacArthur and Wilson 1967) states that biodiversity at a given island is a function of its area and proximity to mainland. Beyond the study of insular communities, the Theory provided a framework to quantify the influence of habitat configuration patterns on biodiversity. More recently, availability of GIS and remote sensing tools have enabled ecologists to measure environmental conditions at very large scales. Moving from single-plot studies, ecologists are increasingly aware that populations and communities are open systems that can be highly

influenced by landscape connectivity (Taylor et al. 1993). The absence of well-defined habitat islands has not precluded ecologists from applying the ideas of island biogeography to terrestrial ecosystems. The solution was to define discrete habitat units analogous to islands, or "patches" (Wiens 1976). Using this definition, "local" processes operate within the patch, and "regional" processes operate outside the patch. I call this procedure the "patch approach".

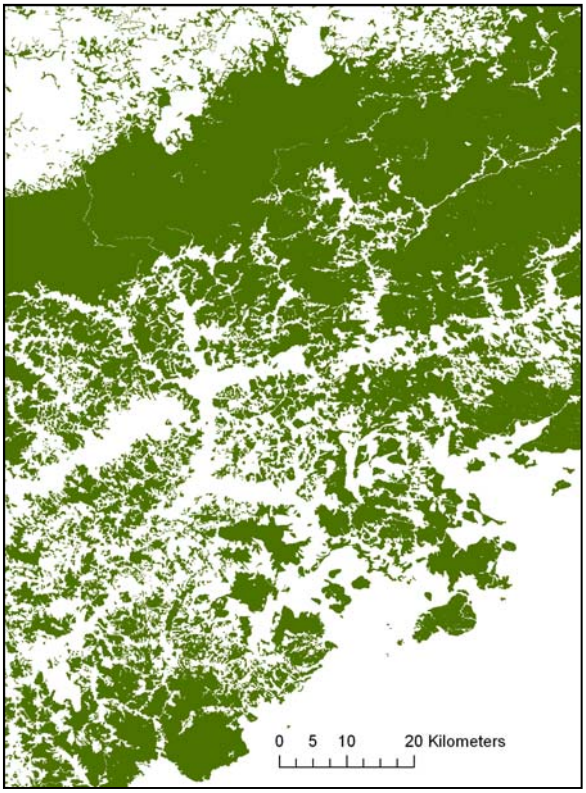
The problem with the patch approach is that the same area can be perceived as one or several patches, depending on the process and the organism under study. Considering the process of foraging, a butterfly finds many foraging patches within a forest tract, whereas a jaguar sees a collection of forest tracts as a single foraging patch. This has motivated the concept of ecological neighborhoods (Addicott 1987, Wiens 1989). The ecological neighborhood refers to an organism-centered procedure to measure environmental pattern. It is defined by an ecological process, a time scale over which the process occurs, and the organism's activity during that time interval (Addicott 1987). One of its main drivers is an organism's dispersal ability. Due to the difficulty in obtaining detailed data on dispersal, the models presented here measure patterns at multiple scales reflecting potential ecological neighborhoods. Models can be subsequently validated with data that is more easily obtained than direct dispersal measures, namely capture success at different points in space.

MEASURES OF HABITAT COVER

The objective of the second chapter is to quantify the effect of forest cover on frugivore bats inhabiting a fragmented forest in Mexico. Several community studies in the Neotropics have shown important differences in community richness and diversity stemming from habitat fragmentation (e.g., Cosson et al. 1999; Schulze et al. 2000, Estrada and Coates-Estrada 2002). This suggests that bat species have different sensitivities to habitat loss and fragmentation. However, researchers are rarely able to quantify how particular species respond to forest cover (but see Gorresen et al. 2005). This lack of scientific information can hinder the prioritization of species for conservation.

Implementation of the patch approach might have prevented researchers from detecting significant relationships, for two main reasons. First, patches are not discrete "islands" in a sea of unsuitable habitat (e.g. Figure 1-1). The intervening habitat between patches can have trees, and patches can be connected by tree lines and riparian habitat. Second, what constitutes a foraging patch from a bat's perspective is expected to be influenced by its diet, morphology, and flying behavior. To tackle this problem, I have employed scale-sensitive measures of forest cover that reflect potential ecological neighborhoods of different frugivore bats.

Figure 1-1: A fragmented landscape in Sao Paulo, Brazil. Green color represents forested areas.



The difficulties imposed by the patch approach can be illustrated by the recent work by Henry et al. (2007). The authors estimated abundance of the large fig eater, *Artibeus jamaicensis* in French Guiana. Forest patches were delimited by the authors and further classified into "continuous forest" or "fragments" according to size. Fragments were located less than 1 km from the continuous forest. Bats were more frequently found in the continuous forest, and this was taken to be evidence of sensitivity to fragmentation. However, sex ratio estimates and physiological measures indicated that the population was not under stress. The authors concluded that bat abundance was misleading as a measure of fragmentation. In fact, the method used to measure landscape pattern

produced misleading conclusions. The categories "continuous forest" and "fragment" reflect the bias of the researcher and not the amount of forest cover that was available to individuals *Artibeus jamaicensis*. The distance between capture points lied well within the home range of a single individual (> 1km; Morrison 1978a,b), thus individuals probably perceived all capture points in the study area as a single foraging patch. The fact that *Artibeus jamaicensis* was more frequently captured in the continuous forest is more likely to result from differences in habitat quality and the species' preference for foraging in mature forest.

Chapter two results demonstrate the usefulness of a flexible, simple approach to measure landscape pattern: the grid approach. There are important differences from the patch-based approach (Table 1-1). Pattern is measured at several scales, instead of using the dichotomy of "local" versus "regional", or "fragment" versus "continuous forest". As a result, there is no effort to quantify the separate contribution of patch area and connectivity (as in metapopulation models; Hanski 1994). Also, the grid approach produces hypotheses about the processes driving a species' response to habitat cover. That is, the relationship between organism abundance and forest cover is strongest when the latter is measured at the scale species utilize the landscape. From a practical perspective, the grid approach uses a reproducible method to measure environmental pattern, whereas the patch approach relies on the researchers' definition of discrete habitat units. Thus, I conclude that if grid maps of forest cover are available, the grid approach should be used to study the effects of habitat loss and connectivity on individual species.

Using bats as a study system opens the possibility to find ecological traits that drive species' sensitivity to forest fragmentation. Two main questions follow from chapter two's work. First, which traits correlate with the scale at which species respond to forest cover? Candidate traits are body size, wing morphology, and diet – traits that collectively influence bats' movement behavior (Aldridge and Rautenbach 1987). Second, does a small ecological neighborhood imply higher sensitivity to fragmentation? It is possible that traits influencing a species' movement behavior also constrain their ability to cross open areas. The use of the grid approach should dramatically increase our ability to investigate these questions.

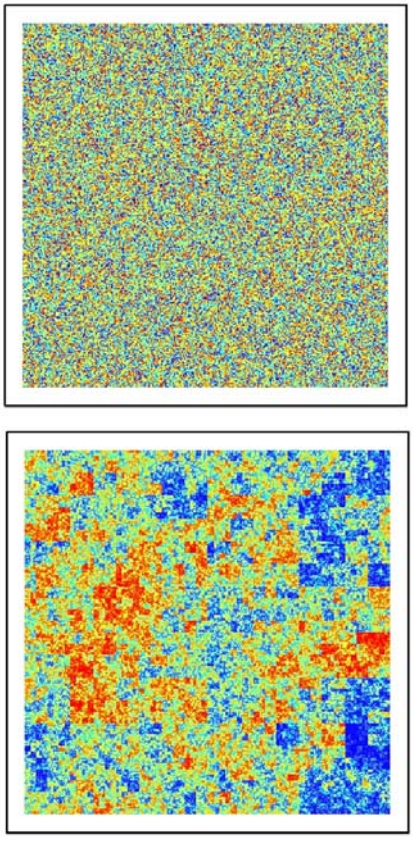
THE EMERGENCE OF DISPERSAL CORRIDORS

Chapter three looks at large-scale corridors in fragmented landscapes. The importance of corridors in conservation biology has been greatly emphasized over the last two decades (reviewed by Chetkiewicz et al. 2006). Researchers have asked whether corridors should be wide or narrow, representing potential habitat or merely conduits for dispersing organisms (Hess and Fischer 2001). Another important line of research investigates the role of corridors in maintaining ecosystem services (Tewksbury et al. 2002). Less often asked is how corridors emerge in the first place, from the interaction between landscape structure and species' traits.

Following the patch approach, researchers traditionally classify the landscape into two categories: "habitat patches" and "matrix" (Figure 1-2). Although habitat patches are usually defined based on minimum area, there might be qualitative differences between "patch" and "matrix" habitat. That is, the matrix is primarily used for dispersal, and thus

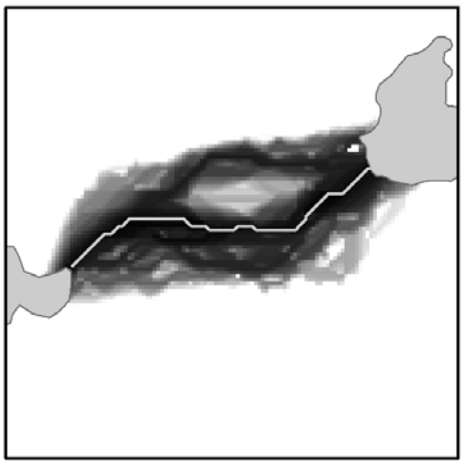
organisms should use a straight-line route when moving in this habitat. Natural landscapes are likely to display a continuum between "patch" and "matrix" habitat. To incorporate this fact, I construct artificial landscapes where the spatial distribution of suitable habitat ranges from random to clumped. Using a graph-theoretical approach, I formalize the above ideas and show that when the distribution of suitable habitat is random (matrix-like), corridors are composed of several straight-line routes. On the other hand, when the distribution of suitable habitat is clumped (patch-like), corridors deviate from straight-line routes and closely follow areas of suitable habitat.

Figure 1-2: The "matrix" (top) versus "patch" (bottom) dichotomy.



Grids have been widely used to model animal dispersal. For example, researchers have studied the influence of landscape fractal dimension on movement patterns (With et al. 1999). The approach presented here is novel in its use of grids to characterize potential corridors. I introduce two corridor characteristics: heterogeneity and redundancy. Corridors are heterogeneous because they are composed of dispersal routes with different quality. Furthermore, the spatial distribution of dispersal routes determines whether corridors are more or less redundant. Redundant corridors contain many disjoint dispersal routes, whereas non-redundant corridors contain close dispersal routes, or dispersal routes that merge forming bottlenecks (Figure 1-3).

Figure 1-3: Example of a corridor connecting two protected areas (gray polygons). The corridor contains two dispersal routes (dark areas) that join forming dispersal bottlenecks. The gray line represents the optimum route between the two protected areas.



The grid-based method used in chapter three translates data on species' habitat preferences into large-scale depictions of connectivity. Results show multiple dispersal routes that can represent alternative management strategies. And as with chapter two, models can be validated with capture data that is easier to obtain than direct measures of organism dispersal.

GRID-BASED APPROACHES IN ECOLOGICAL NICHE MODELING

The objective of the last chapter is to study the correlates of density of five primate species inhabiting a highly fragmented landscape in Brazil. One main challenge of ecological niche modeling is to define the candidate variables that potentially explain observed patterns. In disturbed landscapes, populations are expected to be affected by the anthropogenic context – the economy and the degree of urbanization in the cities containing study sites. However, most attempts to model abundance in disturbance landscapes include data on environmental conditions only.

GIS offer tools to measure variables acting at a study site, or within a given distance from the study site. For example, using road maps and census of human populations, I have estimated the number of people that could travel to study sites via roads in a particular time interval. However while census studies are carried out at the local level, data are usually reported for individual "patches". That is, density data and environmental data are averaged for particular protection areas or forest fragments. This imposes two main limitations on ecological niche modeling: (i) it increases measurement error and (ii) it reduces our ability to make prediction. This is because measures of patch properties rely on the researcher's method to define patches, an issue that has been discussed in the previous sections. Still, the lack of synthetic studies in Neotropical ecosystems raises the need to make the most of existing data.

Here, I have used a grid-based approach to perform ecological niche modeling. To decrease measurement error, I located census trails whenever possible. Furthermore, both models and prediction were built on a grid where each pixel contains information on local environmental conditions, as well as social and economic indicators. Compared to

the patch approach, this procedure has greatly increased model accuracy. This was expected since protected areas traditionally defined as "patches" are rather large (> 40 km^2). Within-patch variation in environmental conditions (e.g., slope and elevation) can be comparable to between-patch variation, thus aggregating data at the patch level leads to loss of information. In addition, the analysis has revealed that primate species display different responses to the anthropogenic context. For example, density was sometimes higher in urban zones, and sometimes higher in rural areas.

MOVING TO GRID-BASED MEASURES OF LANDSCAPE PATTERN

This dissertation illustrates situations in which measuring pattern is critical for understanding process. Although researchers recognize that forest fragments are not islands, the patch approach is rarely questioned. The results shown here emphasize that the grid approach can provide better insight on the biological processes leading to species' abundance and movement patterns. What's more, informative results are more likely to be obtained when pattern is measured at multiple scales. In the context of fragmentation studies, the scale at which species respond to forest cover may shed light on the ecological processes driving species' sensitivity to fragmentation.

Table 1-1: Summary of differences between patch and grid approaches to describe landscape pattern.

Patch approach	Grid approach
Use arbitrary minimum area to define a patch.	Patches emerge when the spatial distribution of suitable habitat creates clumps that meet a species' ecological neighborhood.
"Habitat Patches" versus "Matrix" dichotomy.	"Random" to "Clumped" habitat distribution, with all frequencies in between.
Abundance data averaged within patches.	Report data and coordinates of each sampling site.
Habitat cover defined in terms of "fragment" vs. "continuous forest".	Calculate the amount of forest at varying distances from the sampling site.
Habitat quality averaged for the entire patch.	Measure environmental conditions at varying distances from the sampling site.

LITERATURE CITED

Addicott JF et al. (1987) Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340-346.

Aldridge HDJN, Rautenbach IL (1987) Morphology, echolocation, and resource partioning in insectivorous bats. Journal of Animal Ecology 56: 763-778.

Chetkiewicz CLB et al. (2006) Corridors for conservation: integrating pattern and process. Annual Review of Ecology and Systematics 37: 317-342.

Cosson JF et al. (1999) Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. Journal of Tropical Ecology 15: 515-534.

Estrada AJ, Coates-Estrada R (2002) Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biological Conservation 103: 237-245.

Hanski I (1994) A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151-162.

Henry M et al. (2007) Abundance may be a misleading indicator of fragmentation-sensitivity: the case of fig-eating bats. Biological Conservation 139: 462-467.

Hess GR, Fischer RA (2001) Communicating clearly about corridors. Landscape and Urban Planning 55: 195-208.

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Morrison DW (1978a) Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. Ecology 59: 716-723.

Morrison DW (1978b) Influence of habitat on the foraging distances of the fruit bat, *Artibeus jamaicensis.* Journal of Mammalogy 59: 622-624.

Schulze MD et al. (2000) A comparison of the phyllostomid bat assemblages in undisturbed Neotropical forest and in forest fragments in a slash-and-burn farming mosaic in Peten, Guatemala. Biotropica 32: 174-184.

Taylor PD et al. (1993) Connectivity is a vital element of landscape structure. Oikos 68: 571-573.

Tewksbury JJ et al. (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. Proceedings of the National Academy of Sciences 99: 12923-12926.

Wiens JA (1976) Population responses to patchy environments. Annual Review of Ecology and Systematics 7: 81-210.

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 4: 385-397.

Wiens JA et al. (1993) Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

With KA et al. (1999) Movement responses to patch structure in experimental fractal landscapes. Ecology 80: 1340-1353.

Chapter 2: Scale-dependent Responses to Forest Cover Displayed by Frugivore Bats

ABSTRACT

Despite vast evidence of species turnover displayed by Neotropical bat communities in response to forest fragmentation, the exact shape of the relationship between fragment area and abundance for individual bat species is still unclear. Bats' ample variation in diet, morphology, and movement behaviour can potentially influence species' perception of the landscape. Thus, studies describing fragment area at a single spatial scale may fail to capture the amount of forest available from the perspective of individual bat species. In the present paper, we study the influence of forest cover on bats inhabiting a fragmented forest in Mexico, focusing on some of the most common frugivore species: *Artibeus jamaicensis*, *Carollia* spp. (*Carollia brevicauda* / *Carollia perspicillata*), and *Sturnira* spp. (*Sturnira lilium* / *Sturnira ludovici*).

We quantified forest cover at scales ranging from 50 to 2000 meters, and measured the influence of forest cover on bat capture success, a surrogate for abundance. The three species displayed positive and significant scale-dependent associations with forest cover. Abundance of *Artibeus jamaicensis* increased with forest cover measured at scales ranging between 500 and 2000 m, while *Carollia* spp. responded more strongly to variation in forest cover measured at scales 100-500 m. For *Sturnira* spp., abundance was a function of presence of creeks near mist-netting sites, and amount of secondary forest present at a 200 m scale. The observed variation in responses to forest cover can be explained in light of interspecific differences in diet, home range, and body size. Our results illustrate a method for measuring the effect of forest fragmentation on mobile species and suggest that changes in abundance in fragmented landscapes emerge from the interaction between species' traits and landscape structure.

INTRODUCTION

Patchiness is a pervasive pattern in ecology that can be described at a range of spatial scales (Levin 1992; Keitt and Urban 2005). When foraging, individuals must adjust their movement behaviour according to the level of patchiness in resource distribution, and as a result species display adaptations pertaining to dispersal, sensory, and cognitive abilities that dictate their ecological neighbourhood (Addicott 1987; Wiens 1989). Thus species differing in natural history traits are expected to respond to a distinct subset of scales in resource distribution. Vertebrate body mass is a good predictor of home range size (McNab 1963; Swihart et al. 1988; Minns 1995). For bats, the influence of body mass on movement and foraging behaviour has been extensively studied (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). Nevertheless, the implications of these relationships for the study of species' response to habitat fragmentation has been little explored. Bat census studies in the Neotropics have revealed important differences in community diversity and composition between fragments and continuous forest (Cosson et al. 1999; Schulze et al. 2000, Estrada and Coates-Estrada 2002; Pineda et al. 2005; Faria 2006; Montiel et al. 2006), but in contradiction few studies (Gorresen et al. 2005) have detected a significant effect of fragment area on the abundance of individual bat species. It is possible that, by measuring habitat availability at a single scale, most bat survey studies fail to take into account interspecific differences in ecological neighbourhood.

We focus on species of frugivore bats (family Phyllostomidae) that are common throughout the Neotropics: *Artibeus jamaicensis* (Leach), *Carollia brevicauda* (Schinz), *Carollia perspicillata* (Linnaeus), *Sturnira lilium* (Geoffroy) and *Sturnira ludovici* (Anthony). The target species have similar uses of the vertical strata: they are considered gleaning species (Kalko et al. 1996) that fly in the understory and are frequently captured

using ground mist-nets (Bonaccorso 1979; Simmons and Voss 1998; Bernard 2001). However, there are important differences in the spatial distribution of their preferred food items. *Artibeus jamaicensis* consumes fruits from late-successional trees such as *Ficus* spp. (Morrison 1978a; Bonaccorso 1979). This preference for a food resource that has a scattered distribution is associated with a larger body mass and home range (Morrison 1978a). On the other hand, species from the genus *Carollia* frequently feed on early-successional plants such as *Piper* spp. (Heithaus and Fleming 1978; Marinho-Filho 1991). *Sturnira* shows a preference for *Solanum* spp. fruits (Marinho-Filho 1991) and is commonly found in early-successional areas near creeks (Emmons and Feer 1997). This variation in resource distribution is likely to influence the scale at which species perceive the landscape, thus scale-sensitive measures of habitat availability are warranted when modeling the causes of variation in bat abundance.

In this paper, we have modeled the relationship between bat capture success (a surrogate for abundance) and forest cover measured at several spatial scales in a tropical rainforest in Mexico. Here, the term "scale" is equal to focus, the scale at which grains are aggregated (*sensu* Scheiner et al. 2000), and "grain" refers to the standardized unit used to count the variable of interest (Scheiner et al. 2000) – in our case, "grains" are pixels from a satellite image that are classified as "forest". In practice, scale is equated with the radius used to define the area over which forest cover is calculated. Our goal was to use a species-centered approach to quantify the responses to habitat loss displayed by individual bat species.

METHODS AND ANALYSES

Field Site

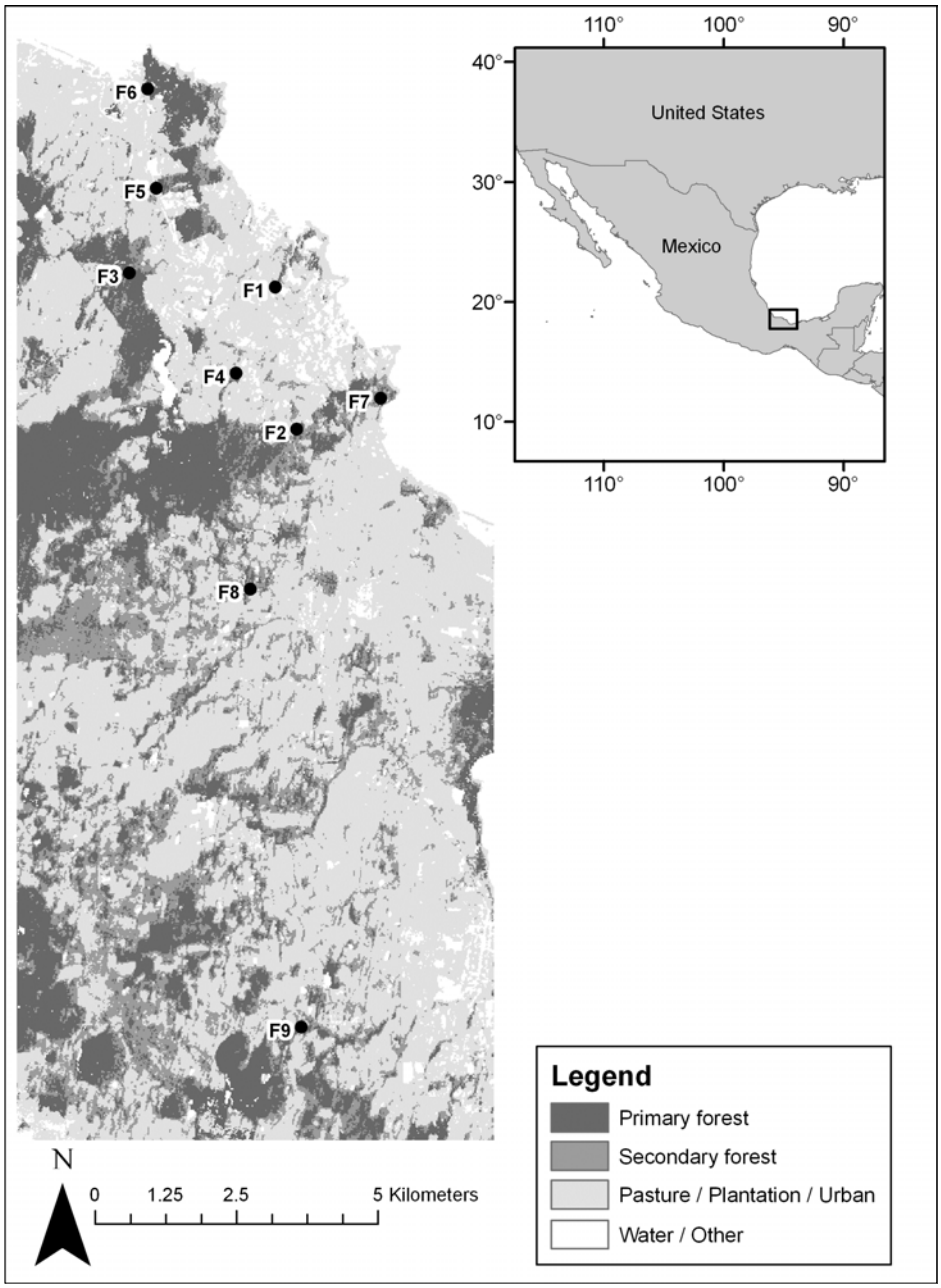
Field work was carried out between June and August 2005 in the region of Los Tuxtlas (Figure 2-1) in the municipality of San Andres Tuxtla, Veracruz, Mexico (18°25' N , 95°00' W), a region harbouring the northern limit of lowland Neotropical rainforest. The mean temperature ranges from 24 to 26 °C and annual precipitation ranges between 3000 and 4500 mm (Soto and Gama 1997). Bat sampling was performed in privately-owned farms located in the "Los Tuxtlas" Biosphere reserve, in an area adjacent to a 3500-ha forest that includes the Biological Field Station Los Tuxtlas of the University of Mexico (UNAM).

Bat Species and Mist-netting

The bat species used in the present study are abundant in Los Tuxtlas. Individuals have been captured in continuous forest as well as in fragments (Estrada and Coates-Estrada 2002) and represent important seed dispersers in this ecosystem (Galindo-Gonzalez et al. 2000). The mean body size in grams is 46.1 for *Artibeus jamaicensis*, 19.5 for *Carollia perspicillata*, 18.5 for *Carollia brevicauda*, 17.6 for *Sturnira lilium*, and 23.2 for *Sturnira ludovici* (Estrada and Coates-Estrada 2002). Due to difficulty identifying individuals, we have pooled data for sister species and will therefore report results for *Carollia* spp. and *Sturnira* spp.

We captured bats in 9 sites (F1 – F9; Figure 1-1) using mist-nets. Each site was sampled for 2 consecutive nights, starting 15 minutes after sunset and lasting 5 hours. Two 2 x 12m mist nets (ATX, Association of Field Ornithologists, MA, USA) were

Figure 2-1: Study site in Los Tuxtlas, Mexico, showing the nine sampling points labeled as F1– F9.



placed 3-5 m apart and within 25 m of the border of a forest fragment and along a trail. In 4 fragments, mist-netting was performed within 20 m of a creek. Sampling was interrupted in nights of full moon (due to bat lunar phobia) and during heavy rain. Each individual was identified to species and we determined its sex, age (adult or juvenile), and if female we assessed its reproductive status (pregnant, lactating or non-reproductive). Individuals were also weighed to the nearest 0.5 gram. Bat capture success for each site was calculated as the number of captured individuals divided by the number of net-hours, the number of open nets times the number of hours nets were open.

Analyses

The study site was characterized using a SPOT 3 satellite image taken in 2005 containing 3 spectral bands and 20 m spatial resolution. We performed unsupervised classification using the method ISOCLUSTER from Idrisi (Clark Labs, MA, USA) and the resulting distribution of land cover classes was consistent with aerial photographs of the study area. This classified image was further processed to produce a map with three land cover classes: (1) primary forest, (2) secondary forest, and (3) "other", including urban areas, crop plantations, pastures, and water (Figure 2-1).

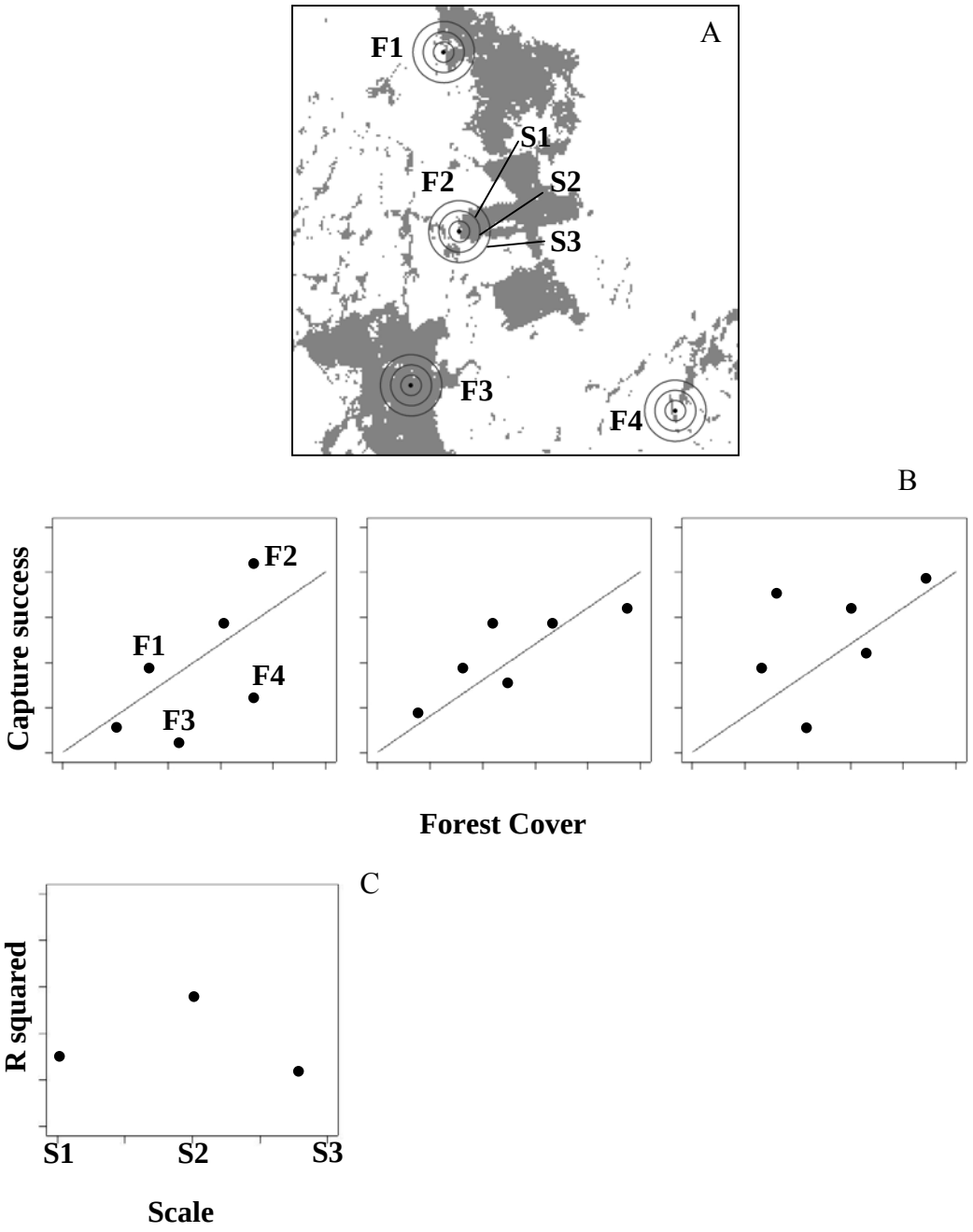
Forest cover around all sampling sites was quantified by defining several circles, each one centered where mist nets were located (Figure 2-1) and with radii ranging from 50-2000 m (inclusive) at intervals of 50 m. For each radius, we calculated the number of 20 m x 20 m pixels classified as "forest" inside each of those circles. Three forest cover values were produced for each scale: primary forest, secondary forest, and primary + secondary. These quantities represent the amount of potential bat habitat associated with spatial scales ranging from 50 m to 2000 m. Besides forest successional stage, one important difference among fragments was the presence of creeks near mist-netting sites.

Thus, another predictor variable of bat abundance was “creek presence”, with possible values 0 (absent) and 1 (present).

We used linear regression to model the relationship between capture success and forest cover, performing one regression for each spatial scale and each forest successional type. Values of R squared and P were computed for each regression, and slope estimates were inspected in order to determine whether bat abundance had a positive or negative relationship with forest cover. The scale for which the largest value of R squared was found was taken as the scale at which species displayed the strongest response to forest cover (Figure 2-2).

The importance of spatial autocorrelation was assessed using Mantel’s permutation test (Mantel 1967). Regression residuals were spatially correlated for *Artibeus jamaicensis* (Mantel test, $P < 0.05$), thus for this species we employed a conditional autoregression (CAR, Cressie 1993). CAR is a linear model that partitions the response variable into trend (the spatially-independent component), signal (the spatial component), and noise, taking into account the proximity between sampling points. In this case, we report the log likelihood as the estimate of model fit, and p-values associated with the slope of the trend term. In all regressions, we used a significance level of 0.05. The language R (R Development Core Team 2008) was employed to measure forest cover and to perform all statistics.

Figure 2-2: Schematic example showing the procedure to measure scale-dependent associations with forest cover. (A) Four mist-netting sites are shown on the map (F1-F4). For each site, forest cover is measured at increasingly larger scales, labeled as S1, S2, and S3. (B) One linear regression "bat capture success x forest cover" is performed at each scale. The fit of the regression (R squared or Log likelihood) is computed. (C) Plots of scale x regression fit may show a peak representing the scale at which the species display the strongest response to forest cover.

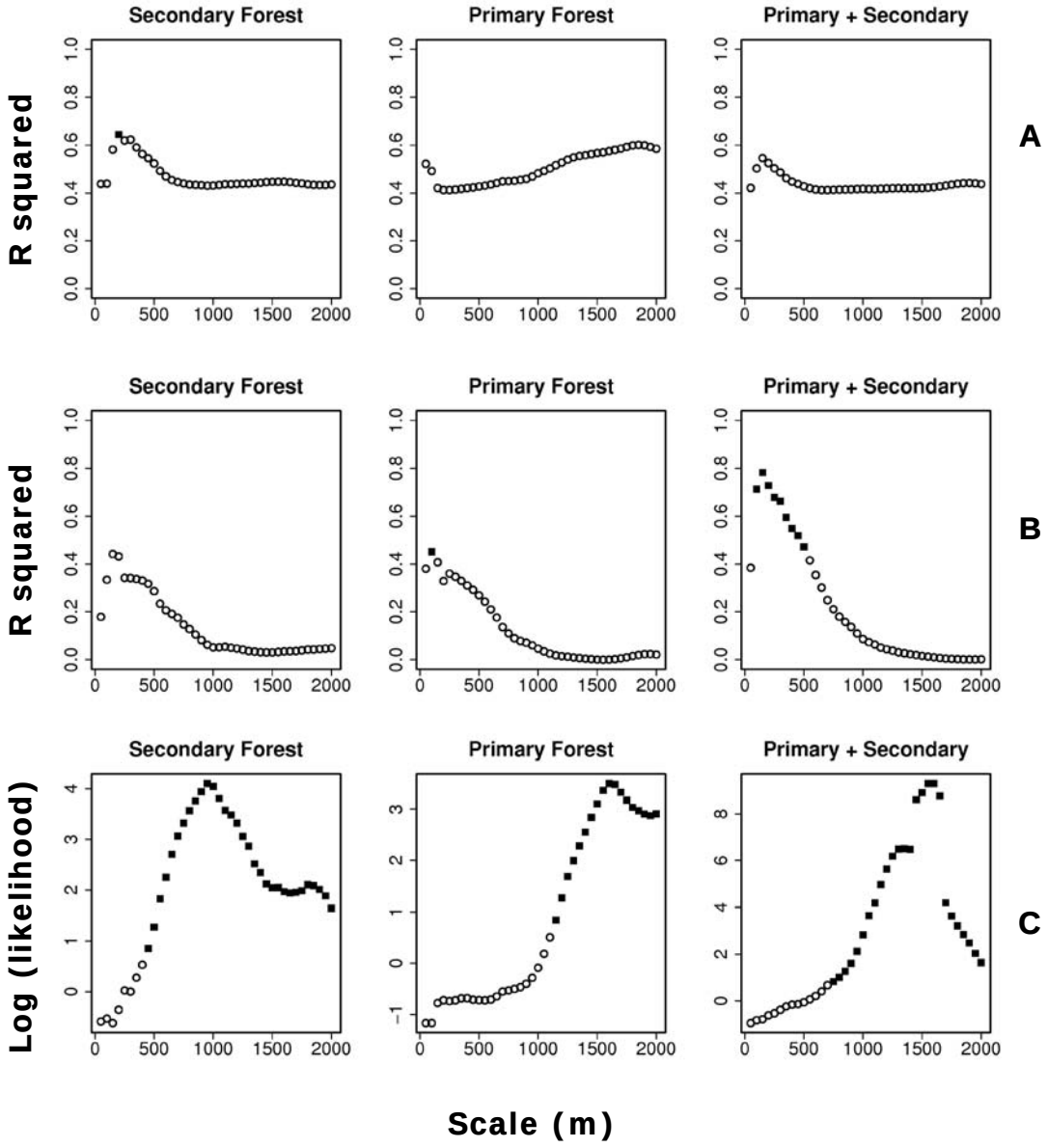


RESULTS

Captures totaled 135 for *Carollia* spp., 71 for *Artibeus jamaicensis*, and 143 for *Sturnira* spp.. The number of net hours per site ranged from 13 to 19 (mean = 16.25). A positive and significant relationship between forest cover and capture success was found for all three groups, however species responded differently to forest successional stages and scale of measurement of forest cover. Adding the variable "creek presence" did not have a substantial impact on the fit of the models for *Carollia* spp. or *Artibeus jamaicensis*, thus this variable was only used to model abundance of *Sturnira* spp..

We obtained one significant model for *Sturnira* spp. relating abundance to the presence of a creek near mist-netting sites, and amount of secondary forest measured at a 200 m scale ($R^2 = 0.64$; $P = 0.044$; Figure 2-3a). The species *Carollia* spp. responded to small-scale variation in forest cover (Figure 2-3b). A stronger relationship between abundance and forest cover was obtained when successional stages were aggregated (primary + secondary forest) and at scales ranging between 100 and 500 m (inclusive). In the regression for *Artibeus jamaicensis*, we removed one point consisting of a site (F1) where the netting was performed adjacent to a day roost. *A. jamaicensis* displayed a positive relationship with both primary and secondary forest (Figure 2-3c). Differently from *Sturnira* spp. and *Carollia* spp., *A. jamaicensis* responded to large-scale variation in forest cover (450 – 2000 m; Figure 2-3c). In addition, *A. jamaicensis* was differentially influenced by primary and secondary forest. The strongest correlation between bat capture success and forest cover was observed when primary forest was measured at a 1500 m scale, and secondary forest was measured at a 1000 m scale.

Figure 2-3: Variation in regression fit from models relating forest cover and bat abundance. (A) *Sturnira* spp., (B) *Carollia* spp., (C) *Artibeus jamaicensis*. Closed squares indicate significant models ($P < 0.05$) and open circles indicate non-significant models ($P > 0.05$).



DISCUSSION

We have studied responses to forest cover displayed by three common bat genera in a tropical fragmented landscape in Los Tuxtlas, Mexico. In agreement with studies performed in a subtropical forest (Gorresen et al. 2005), bats displayed scale-dependent responses to forest cover. Abundance for *Carollia* spp. and *Sturnira* spp. was a function of small-scale variation in forest cover (Figures 2-3a, 2-3b), while abundance measured for *Artibeus jamaicensis* was largely a function of large-scale variation in forest cover (Figure 2-3c). *Sturnira* spp. responded to a very narrow range of spatial scales (Figure 2-3a). For this species, local conditions were as important as the distribution of forested areas in predicting abundance patterns: significant models were obtained only after taking into account the presence of creeks near mist-netting sites.

Frugivore bats do not present a single spatial scale of movement. Fine-scale movements include daily commuting from a day roost to a feeding area and movement between feeding areas and night roosts (Emmons and Feer 1997). Bats also perform large-scale movements, including exploratory flights and roost changes (Heithaus and Fleming 1978; Bernard and Fenton 2003). Due to the small temporal scale of our study, it is reasonable to expect our results to reflect differences in fine-scale movements that occur daily than occasional exploratory flights and roost changes. In fact, results for *Carollia* spp. and *Artibeus* spp. are consistent with differences in commuting distances. In Los Tuxtlas, female *A. jamaicensis* have been observed to fly an average of 8 Km between day roosts and feeding areas (Morrison 1978b), whereas radio tracking studies in Costa Rica estimate an average distance of 0.81 Km between day roosts and feeding areas for *Carollia perspicillata* (Heithaus and Fleming 1978).

When quantifying forest cover, we produced separate estimates for primary and secondary forest. In general, abundance for *Carollia* spp. increased with estimates of

forest cover that aggregated both successional stages (Figure 2-3a). One possible interpretation of this result is that the combination of primary and secondary forests forms a more continuous habitat than either classes alone (Figure 2-1), and habitat connectivity is more important than successional stage for this species. Abundance of *Sturnira* spp. increased only with amount of secondary forest (Figure 2-3b), which reflects its preference for shrubs that grow in early-successional habitats. Abundance of *A. jamaicensis* increased significantly with both primary and secondary forest (Figure 2-3c). This confirms this species' status as a habitat generalist (Bonaccorso 1979). Working with bat communities in Barro Colorado Island, Kalko et al. (1996) placed Neotropical frugivore bats in the "highly cluttered frugivore" foraging guild, while obstacle course experiments suggest that *A. jamaicensis* is less efficient in negotiating obstacles in highly cluttered habitats (Stockwell 2001). In many disturbed areas such as Los Tuxtlas, the availability of trails that can be used as flyways may facilitate or enable the use of secondary forest by *A. jamaicensis*.

Changes in bat communities due to forest fragmentation have been widely documented in the Neotropics (Cosson et al. 1999; Schulze et al. 2000; Estrada and Coates-Estrada 2002; Pineda et al. 2005; Faria 2006; Montiel et al. 2006). But researchers employing single-scaled measures of fragment area have been unable to detect a significant effect of habitat loss on bat abundance (Faria 2006). Using a scale-dependent measure of forest cover has enabled us to predict a large amount of variation in bat abundance (> 70% for *Carollia* spp. and > 60% for *Sturnira* spp.; Figures 2-3a-b). These results support the assertion that grid-based indices are well-suited to study mobile species – particularly central-place foragers – that inhabit complex landscapes where habitat patches are difficult to define (Kremen et al. 2004; Winfree et al. 2005). From a practical perspective, the approach exemplified here facilitates among-site comparisons,

because the task of delineating fragments brings some subjectivity to analyses. We deliberately employed a simple measure of habitat availability which might not be appropriated for less common, specialist bat species. One possible modification of the metric used here is to weight each habitat pixel by its estimated quality (Betts et al. 2006) or by the relative cost to reach it given a movement model (Verbeylen et al. 2003; Drielsma et al. 2007).

Our results illustrate a simple approach for quantifying the effects of habitat fragmentation on mobile species. From a conservation perspective, the species' differential responses to landscape structure observed here may be one of the mechanisms underlying community turnover in fragmented landscapes, a pattern that has been demonstrated for vertebrates and invertebrates in the Amazon (Laurance et al. 2002). Studies with larger number of species and feeding guilds should elucidate whether body mass, diet, and other traits that correlate with movement behavior are in general correlated with bats' responses to landscape structure.

ACKNOWLEDGEMENTS

I would like to thank A. Estrada and M. Ricker for support at the Los Tuxtlas Biological Station, E. Sanchez Vazquez, D. Gallegos Castillo and M. Leoni for assistance in the field, R. Coates for assistance identifying species, and C. Brooks, T. Fuller, and three anonymous reviewers for comments on the manuscript. This work was funded by the Exploration Fund and the Dorothea Bennet Memorial Graduate Fellowship.

LITERATURE CITED

Addicott JF et al. (1987) Ecological neighborhoods – scaling environmental patterns. Oikos 49: 340-346.

Aldridge HDJN, Rautenbach IL (1987) Morphology, echolocation, and resource partioning in insectivorous bats. Journal of Animal Ecology 56: 763-778.

Bernard E (2001) Vertical stratification of bat communities in primary forests of Central amazon, Brazil. Journal of Tropical Ecology 17: 115-116.

Bernard E, Fenton MB (2003) Bat mobility and roosts in a fragmented landscape in central Amazonia, Brazil. Biotropica 35: 262-277.

Betts MG et al. (2006) Independent effects of fragmentation on forest songbirds: an organism-based approach. Ecological Applications 16: 1076-1089.

Bonaccorso F (1979) Foraging and reproductive ecology in a Panamanian bat community. Bulletin of Florida State Museum of Biological Sciences 24: 359-408.

Cosson JF et al. (1999) Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. Journal of Tropical Ecology 15: 515-534.

Cressie NAC (1993) Statistics for Spatial Data. -Wiley.

Drielsma M et al. (2007) A raster-based technique for analyzing habitat configuration: the cost-benefit approach. Ecological Modeling 202: 324-332.

Emmons LH, Feer, F (1997) Neotropical Forest Mammals. A Field Guide. - University of Chicago Press.

Estrada AJ, Coates-Estrada R (2002) Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biological Conservation 103: 237-245.

Faria D (2006) Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. Journal of Tropical Ecology 22: 531-542.

Galindo-Gonzalez J et al. (2000) Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology 14: 1693-1703.

Gorresen PM et al. (2005) Multivariate analysis of scale-dependent associations between bats and landscape structure. Ecological Applications 15: 2126-2136.

Heithaus ER, Fleming TH (1978) Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomatidae). Ecological Monographs 48: 127-143.

Kalko EK et al. (1996) Organization, diversity, and long-term dynamics of a Neotropical bat community. In: Cody M, Smallwood J (eds.), Long-Term Studies of Vertebrate Communities. Academic Press, pp. 503-548.

Keitt TH, Urban DL (2005) Scale-specific inference using wavelets. Ecology 86: 2497-2504.

Kremen C et al. (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters 7: 1109-1119.

Laurance WF et al. (2002) Ecosystem decay of forest fragments: a 22-year investigation. Conservation Biology 16: 605-618.

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

Marinho-Filho JS (1991) The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. Journal of Tropical Ecology 7: 59-67.

McNab B (1963) Bioenergetics and the determination of home range size. American Naturalist 97: 133-140.

Minns CK (1995) Allometry of home-range size in lake and river fishes. Canadian Journal of Fisheries and Aquatic Sciences. 52: 1499-1508.

Montiel S, et al. (2005) Bat assemblages in a naturally fragmented ecosystem in the Yucatan peninsula, Mexico: species richness, diversity and spatio-temporal dynamics. Journal of Tropical Ecology 22: 267-276.

Morrison DW (1978a) Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. Ecology 59: 716-723.

Morrison DW (1978b) Influence of habitat on the foraging distances of the fruit bat, *Artibeus jamaicensis.* Journal of Mammalogy 59: 622-624.

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia: Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B 316: 335-427.

Pineda E et al. (2005) Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. Conservation Biology 19: 400-410.

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-projects.org.

Scheiner SM et al. (2000) Species richness, species-area curves and Simpson's paradox. Evolutionary Ecology Research 2: 791-802.

Schulze MD et al. (2000). A comparison of the phyllostomid bat assemblages in undisturbed Neotropical forest and in forest fragments in a slash-and-burn farming mosaic in Peten, Guatemala. Biotropica 32: 174-184.

Simmons NB, Voss RS (1998). The mammals of Paracou, French Guiana: a Neotropical rainforest fauna. Part I. Bats. Bulletin of the American Museum of Natural History 237: 1-219.

Soto M, Gama L (1997) Climas. In: González-Soriano E, et al. (eds.), Historia Natural de Los Tuxtlas. Universidad Nacional Autonoma de Mexico, Mexico, pp. 7-23.

Stockwell EF (2001) Morphology and flight maneuverability in New World leaf-nosed bats (Chiroptera: Phyllostomidae). Journal of Zoology 254: 505-514.

Swihart RK et al. (1998) Relating body size to the rate of home range use in mammals. Ecology 69: 393-399.

Verbeylen G et al. (2003) Does matrix resistance influence Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? Landscape Ecology 18: 791-805.

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3: 385-397.

Winfree R et al. (2005) Testing simple indices of habitat proximity. American Naturalist 165: 707-717.

Chapter 3: Beyond the Least-cost Path: Two Graph Theory Methods that Assess Corridor Redundancy

ABSTRACT

The impact of the landscape matrix on patterns of animal movement and population dynamics has been widely recognized by ecologists. However, few tools are available to model the matrix's influence on the length, relative quality, and redundancy of dispersal routes connecting habitat patches. Many GIS software packages can use land use / land cover maps to identify the route of least resistance between two points – the least-cost path. The limitation of this type of analysis is that a single path is identified, even though alternative paths with comparable costs might exist. Finding these routes would be of great practical value for studies of animal movement, as well as for conservation initiatives. In this paper, we implemented two graph theory methods that extend the least-cost path approach: the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs) tool. Both methods enable the visualization of multiple dispersal routes that together, are assumed to form a corridor. Using artificial landscapes, we show that corridors containing alternative dispersal routes emerge when good habitat is randomly distributed in space. As patches of favorable habitat start forming, corridors become narrower and less redundant. In addition, we explored the effect of small, localized disturbance on dispersal routes linking conservation units in the Brazilian Atlantic forest. Simulated habitat destruction led to the appearance of alternative dispersal routes, or caused existing dispersal routes to become narrower. The extension of the least-cost path approach enables researchers to visualize redundant dispersal routes and areas acting as dispersal bottlenecks, as well as calculate confidence intervals on the estimated length and cost of least-cost paths.

INTRODUCTION

The landscape matrix can play a fundamental role in shaping animal movement patterns. Ecological models that specify the effect of matrix heterogeneity on movement rates can more successfully predict patch occupancy (Ricketts 2001; Verbeylen et al. 2003), metapopulation dynamics (Vandermeer and Carvajal 2001), and gene flow (Stevens et al. 2006). Population persistence in fragmented landscapes is also influenced by organisms' tolerance of the matrix (Laurance et al. 2002). Furthermore, the role of behavior and natural history in shaping species' responses to the matrix has motivated the concept of functional connectivity (Calabrese and Fagan 2004). While many field studies have described the influence of different land cover types in channeling or repelling movement of particular species (e.g., Burel 1996; Lees and Peres *in press*), few tools are available to integrate data on matrix heterogeneity and species' habitat preferences to model the length, relative quality, and redundancy of large-scale dispersal routes.

When attempting to predict dispersal routes, one is faced with the constellation of models used to study movement in nature (reviewed in Turchin 1998). Here, we employ a movement model that assumes successfully dispersing organisms are more likely to use the route of least resistance when moving between two points, or the least-cost path. Despite its simplifying assumptions, the least-cost path has been used to predict patch occupancy (Chardon et al. 2003; Verbeylen et al. 2003) and inter-patch movement rates (Sutcliffe et al. 2003). The least-cost path is identified using a graph theory algorithm, Dijkstra's breadth-first search (Cormen et al. 2001). Many GIS software packages have functions to locate the least-cost path between two points. Usually, the input is a grid map of values that represent the relative cost to cross each cell in any direction. Although only one path is obtained, Dijkstra's algorithm can be easily modified to output multiple paths with similar costs.

Ecologists and managers would greatly benefit from the ability to identify multiple dispersal routes linking habitat patches. There is evidence that dispersing organisms use better than random routes, but not necessarily the best route (Driezen et al. 2007), and connectivity measures focusing on optimum paths fail to incorporate variation in individual behavior (Belisle 2005). From a management perspective, least-cost paths have been employed in the design of linked reserve systems (Hoctor et al. 2000; Schadt et al. 2002; Larkin et al. 2004). This approach, however, can lead to very narrow linkages (Alagador and Cerdeira 2007) that might not be located in land tracts available for purchase. Also, similar landscape elements may differ in their potential to channel dispersing organisms. For example, field studies in Canada (Clevenger et al. 2001) show that drainage culverts can act as habitat linkages for several mammal species, but culverts near roads with higher traffic volume and noise level are less commonly used.

We employ two graph theory methods based on Dijkstra's breadth-first search algorithm (see *Methods*), that can identify multiple dispersal routes with similar costs to the least-cost path. We propose that corridors can contain multiple dispersal routes. However, we do not advocate a method for designing corridors (including few or many dispersal routes), neither do we attempt to quantify corridors' role in conserving biodiversity. Rather, our main objective is to extend the least-cost path approach and be able to produce (i) maps depicting alternative dispersal routes and dispersal bottlenecks, (ii) confidence estimates on the length and cost of least-cost paths. Results were generalized using artificial landscapes. More specifically, we investigated the influence of matrix heterogeneity on the number and spatial distribution of dispersal routes. In addition, our method was illustrated with data from the Brazilian Atlantic forest, a highly fragmented ecosystem located in Brazil's most developed region (Morellato and Haddad 2000). The objective was to explore the effect of habitat loss on corridors linking

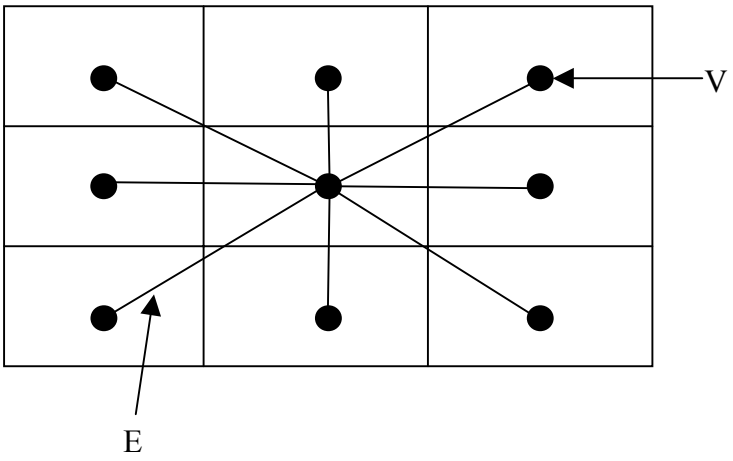
conservation units. Last, we discussed how our approach can be refined and be incorporated in animal movement studies and conservation initiatives.

METHODS AND ANALYSES

The Landscape Graph

In this section, we describe the approach that is routinely employed to perform any type of distance calculations on grids. Most GIS software packages use graphs (Urban and Keitt 2001) to represent grid maps. Graphs are composed of vertices (V) that are placed on cell centers, and edges (E) that connect each vertex to its eight nearest neighbors (Figure 3-1).

Figure 3-1: The landscape graph. In most software packages, grid maps are internally represented as a graph. Vertices (V) are located in cell centers. Each vertex is connected to its eight nearest neighbors by an edge (E). Edge weights (not shown) hold information on the cost to move between pairs of vertices.



Using this representation, we can define two cost grids:

(a) Relative cost grid (Figures 3-2a, 3-3a), also referred to as a friction layer (Verbeylen et al. 2003). Each vertex contains the relative cost to cross it in any direction.

(b) Cumulative cost grid (Figures 3-2b, 3-3b). Consider a source (S) composed of one or more vertices. Each vertex in the cumulative cost grid contains the minimum cumulative cost to reach S. This is calculated in two steps: first, the cost to move between pairs of vertices is stored as edge weights. The weight W for an edge connecting vertices V1 and V2 is calculated as:

$$W = (\text{Relative Cost } (V1) + \text{Relative Cost } (V2)\ ) / 2 \quad (1)$$

For diagonal edges, edge weights W' are calculated as:

$$W' = W * \sqrt{2} \quad (2)$$

Second, Dijkstra's breadth-first search algorithm (Cormen et al. 2001) is used to find the least-cost path between S and each vertex in the graph. The minimum cumulative cost between S and a given vertex (V) is the sum of all edge weights in the least-cost path connecting S and V. The least-cost path between two habitat patches P1 and P2 is calculated by assuming that S = P1 and V = the vertex in P2 that is closest to P1.

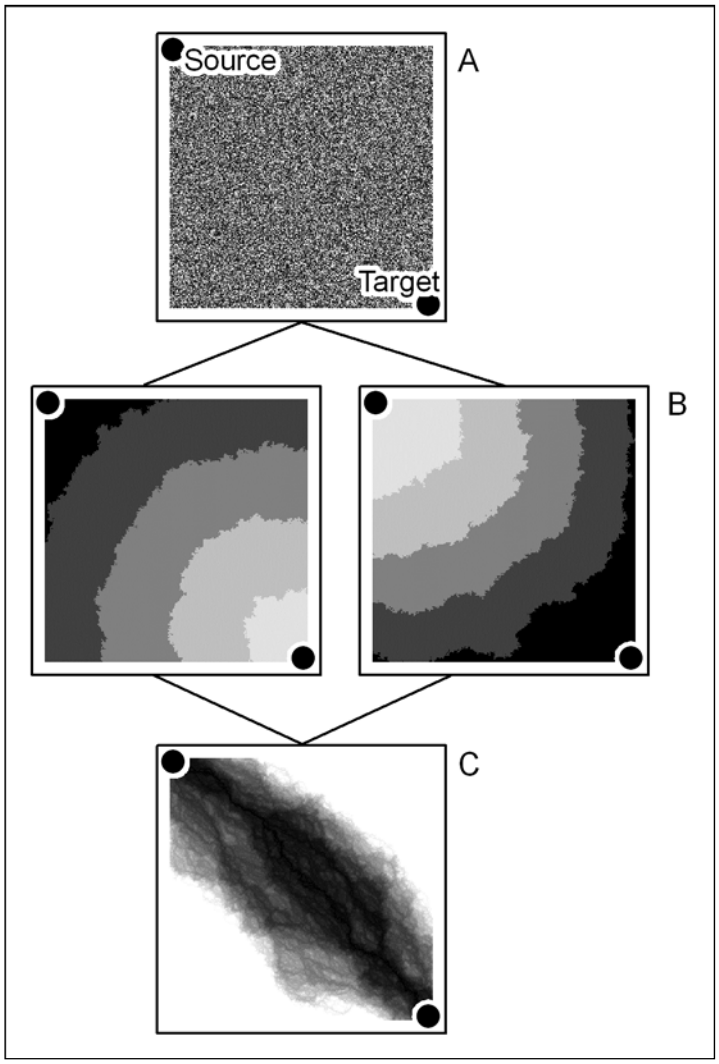
In the next two sections, we build on the above representation and describe two methods that extend Dijkstra's breadth-first search algorithm.

Conditional Minimal Transit Cost (CMTC)

Consider a vertex (V) located between groups of source vertices (S) target vertices (T). The Conditional Minimum Transit Cost (CMTC) for V is the cost-weighted distance to move from S to T, conditional on the route forming the shortest passage between S and T while passing through V. It is calculated as (Figure 3-2):

CMTC (V, S, T) = Cumulative cost (V, S) + Cumulative cost (V, T) *(3)*

Figure 3-2: Illustration of the procedure for calculating the CMTC. (A) Relative cost grid. (B) The cumulative cost grid for the target (left) and the source (right). Lighter shades indicate lower cumulative cost. (C) The two grids from (B) are added to produce the CMTC grid.



By visually inspecting the CMTC grid (Figure 3-2c), one can identify stretches of contiguous cells with low CMTC value. We refer to these cell groups as "dispersal routes", while recognizing that the distinction between routes that are close together is arbitrary. The least-cost path is invariably located within one dispersal route.

The final CMTC grid was obtained by masking out all cells with CMTC values larger than the minimum CMTC value plus 10% (Figure 3-2c). The remaining values were then divided by the grid's maximum CMTC. In practice, obtaining a CMTC grid is straightforward with modules such as Spatial Analyst within ArcGIS (Esri, California). Some conservation biologists strongly advocate the CMTC approach for designing wildlife corridors (www.corridordesign.org), but we were not able to find examples of its application. Also, the relationship between spatial autocorrelation in habitat quality and the distribution of dispersal routes as predicted by the CMTC has not yet been explored (see below: *Applications to artificial landscapes*). We assumed that dispersal routes within the 10% threshold form a corridor, but emphasize that our choice of corridor width was arbitrary.

Multiple Shortest Paths (MSPs)

We wrote a stochastic version of Dijkstra's algorithm (Figure 3-4) that outputs multiple realizations of the least-cost path, or Multiple Shortest Paths (MSPs). As described above, the least-cost path is obtained from a relative cost grid. Relative costs (Figure 3-3a) were allowed to vary between 0 (lowest cost) and 1 (highest cost). Dijkstra's breadth-first search algorithm (Cormen et al. 2001) proceeds by iteratively marking vertices in the order of their cumulative distance from the source. At each step, the algorithm must identify the set of neighbors associated with each marked vertex.

Instead of finding all eight neighbors, we wrote a probabilistic function as follows (Figure 3-3):

(i) Draw a number (U) between 0 and 1 from a random uniform distribution.

(ii) Delete edges in the graph. An edge with weight W connecting two adjacent vertices V1 and V2 is deleted if W > U. That is, connections with lower cost were more likely to be maintained.

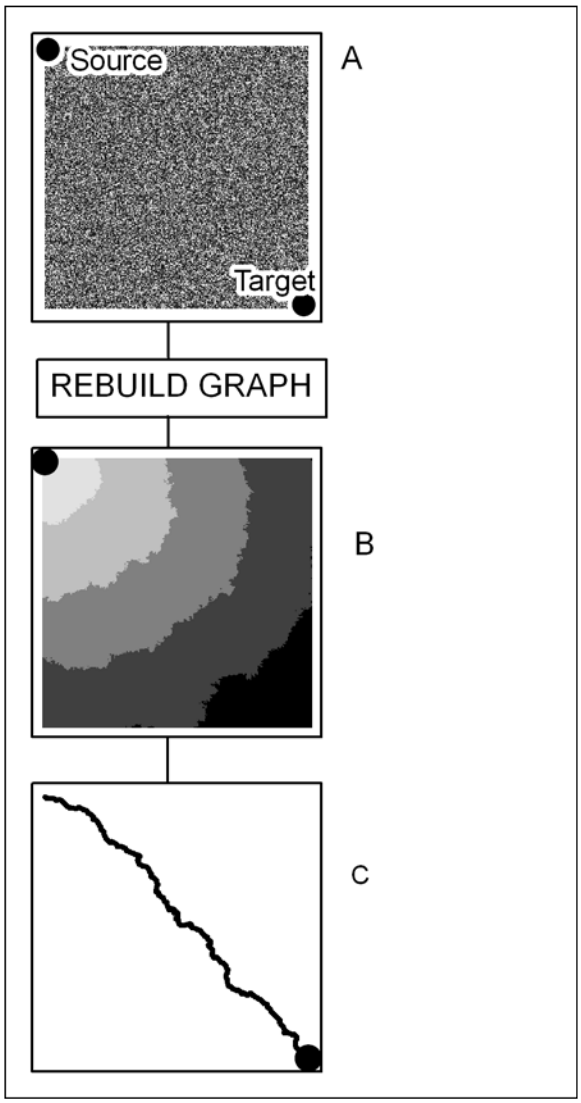
A program implementing Dijktra's algorithm (with the above modification) was run 100 times in order to produce 100 least-cost paths for each study case (Figure 3-3c shows one path). The programs used to obtain both CMTCs and MSPs were written in the Java programming language.

Applications to Artificial Landscapes

We generated five 256 x 256 artificial relative cost grids with different patterns of autocorrelation in cost values. The dominant scale of variation in cost values was manipulated using wavelet transforms (Mallat 1989). We started with a grid containing values between 0-1, drawn from a random uniform distribution. Using this grid, each landscape was created in four steps: (a) apply the discrete Haar wavelet transform; (b) obtain wavelet coefficients; (c) multiply coefficients by 2 ^ (L* ß), where L is the coefficient level; (d) apply the inverse Haar wavelet transform on the modified coefficients.

The values of the parameter ß were 0, 0.25, 0.50, 0.75, and 1. A ß value of zero generates a surface with white noise. As ß increases, patches of favorable habitat start forming. The program for generating artificial landscapes was written in R (R Core Development Team 2008) using functions from the package "waveslim". We calculated the CMTC and MSPs for all five artificial landscapes.

Figure 3-3: Illustration of the procedure for locating MSPs. (A) Relative cost grid. (B) Cumulative cost grid for the source. Lighter shades indicate lower cumulative cost. This was calculated after rebuilding the graph that represents the landscape. (C) With the cumulative cost grid, we trace the least-cost path between source and target. (B) and (C) are repeated 100 times to produce 100 least-cost paths.



Applications to Real Landscapes

We studied a real landscape (Figure 3-4) that covers 111 km^2 of the Brazilian state of São Paulo (upper left coordinates: 23.60S, 49.00W; lower right coordinates: 25.40S, 46.20W). Remaining forests are part of the Atlantic forest biome (for a description, see Oliveira-Filho and Fontes, 2000). Despite its location in highly industrialized São Paulo state, the study area still contains large forest tracts and rural properties. A recent vegetation map (Eva et al. 2002) estimates that 11.1% of the study area is devoted to intensive agriculture, 7% contains a mix of agriculture and degraded vegetation, 23% is a mix of agriculture and degraded forest, and 46 % is covered with forest. Excluding São Paulo's metropolitan area, human populations per municipality range in size from 3403 to 412243 (mean = 60410; IBGE 1991). Five conservation units are considered here: Pedro de Toledo Nucleus within Serra do Mar State Park (868 km^2), Juréia-Itatins Ecological Reserve (801 km^2), Jurupará State Park (259 km^2), Jacupiranga State Park (1552 km^2), and the contiguous units Intervales State Park, Carlos Botelho State Park, Ecological Station Xitué, and Alto do Ribeira Touristic State Park (1282 km^2), referred together here as "Paranapiacaba" due to their location along the Paranapiacaba Valley. Our analyses consist of modeling dispersal routes between all pairs of conservation units.

Three land use / land cover maps were the main input for our analyses.

(iii) The Modis Continous Fields, (Hansen et al. 2003) contains estimates of percent tree cover. Values were manipulated (Table 2-1) in order to obtain a grid with values ranging between 0 (= 100% tree cover) and 1 (= no tree cover).

(iv) The Human Footprint Map (Sanderson et al. 2002) is a global dataset with estimates of anthropogenic impact ranging from 0 (pristine land) to 100 (most

disturbed land), normalized per ecosystem. These estimates were based on patterns of human population density, land use, and transportation networks. We divided original values by 100 (Table 2-1) to obtain a grid with values ranging from 0 (= pristine land) to 1 (= most disturbed land).

(v) The South American Vegetation Map (SAVM; Eva et al. 2002) contains information on forest distribution, degree of forest disturbance, and mixture with agricultural lands. We assigned each class in the SAVM grid (Table 2-1) a relative cost value ranging from 0 (= closed or dense forest) to 1 (intensive land use or non-forested ecosystems).

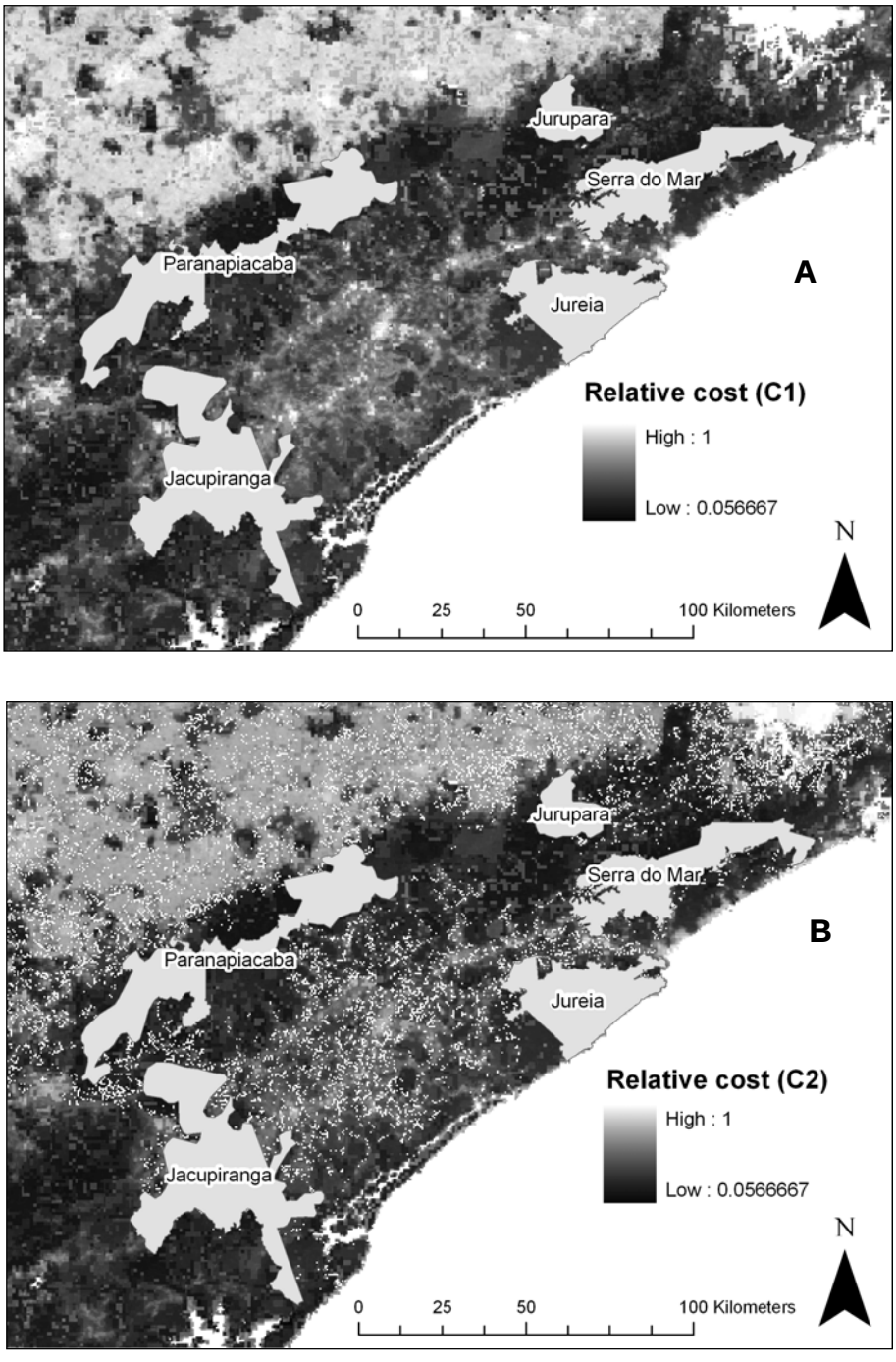
The Footprint and SAVM grids were rescaled so as to bring their spatial resolution to 500 m. Two relative cost maps were produced by combining the three GIS layers described above (Table 3-1). The first relative cost map (C1; Figure 3-4a) was obtained by averaging the average of the values in the three grids described above (Footprint, Modis, and SAVM). As a result, we obtained a grid where cell values ranged from 0.057 (minimum relative cost to cross) to 1 (maximum relative cost to cross). The second cost map (C2; Figure 3-4b) simulated the removal of small forest fragments from C1. This was accomplished in three steps. First, we produced a binary map with areas classified as "forest" or "non-forest" based on the SAVM. This binary map was eroded and dilated by 0.5 pixel, resulting on the deletion of fragments with area < 5 ha and linear elements (such as riparian corridors) < 500 m wide. Last, C2 was obtained by assigning the maximum relative cost (1) to the deleted cells. All other cells contained the same values as C1, and the range of relative cost values for the entire grid remained unchanged (0.057 - 1). It was assumed that individuals could not move through water, thus a cost value of positive infinity was assigned to cells representing water bodies in both C1 and C2 scenarios. Finally, we calculated the CMTC and MSPs for both C1 and C2 scenarios.

All GIS layers were processed using programs written in Java programming language, and illustrations were produced in ArcMap (Esri, California).

Table 3-1: Grids used to construct the relative cost maps used in the present study, their original spatial resolution (pixel size), period of data collection, and operations performed on original grid values.

Layer	Resolution (m)	Years	Operations performed on the original raster values
South America Vegetation Map	1000	1995 - 2000	0 = closed, dense, transitional forest 0.25 = open forest 0.5 = mosaic agriculture / degraded forest 0.75 = shrubland, savannah, grassland 1 = intensive agriculture, mosaic agriculture / degraded vegetation, desert, urban
Human Footprint	1000	1960's - 2001	Final value = (Original Value) / 100
Modis Continuous Fields, % tree	500	2000 - 2001	Final value = (100 – Original Value) / 100

Figure 3-4: Study site in the Brazilian Atlantic forest, showing conservation units in São Paulo State. (A) Relative cost values for scenario C1. (B) Relative cost values for scenario C2 (after deletion of small forest fragments).



RESULTS

When applied to artificial landscapes, the two graph theory approaches proposed here outlined the influence of matrix heterogeneity on the spatial distribution of alternative dispersal routes (Figure 3-4). Landscapes with little autocorrelation in relative habitat quality produced redundant corridors with more alternative dispersal routes (Figure 3-5; ß closer to zero). As patches of favorable habitat started to form, corridors became restricted to fewer routes. This was evidenced in the outputs of both the CMTC and MSPs calculations (Figure 3-5; ß closer to one).

We tested the influence of small, localized disturbance on corridors connecting five conservation units in the Brazilian Atlantic forest (Figures 3-4). Since small fragments were not homogeneously distributed in the study area, corridors obtained under the scenario C1 were differentially affected by simulated fragment removal in scenario C2 (Table 3-2). In most cases, the CMTC grid displayed more than one alternative route between conservation units, one of them being the least-cost path (Figures 3-6a-h). When conservation units were close, the distance between them was small with respect to the variation in their shape. In this case, the CMTC grid produced narrow corridors, coinciding with the links representing the shortest Euclidian distance (Figures 3-6 b, i, j). When corridors contained alternative routes, these were not always disjoint (Figure 3-6a). The constriction zones where dispersal routes merged represented potential dispersal bottlenecks (Figures 3-6c-h). In most cases, the location of the least-cost path did not change substantially as a result of small fragment removal (Figures 3-6a-c; e-g; i-j). But in two cases, the least-cost path for scenario C2 was displaced to an alternative route located a few kilometers away from the least-cost path for scenario C1 (Figures 3-6d, h).

Table 3-2: Conservation units included in the present study. Each unit in a pair can serve as a source or a target for dispersing organisms. The first line contains the straight-line distance between units (in kilometers), and the second line shows the percentage of 500-m2 cells deleted from the corridor as a result of simulating fragment removal.

	Juréia	Jacupiranga	Jurupara	Serra do Mar	Paranapiacaba
Juréia		72.321	35.391	6.905	3.993
		5	3.6	10.4	5.5
Jacupiranga			115.502	104.800	7.868
			4.0	5.0	21.0
Jurupara				7.263	43.739
				2.0	1.2
Serra do Mar					51.183
					2.3

Figure 3-5: Influence of landscape patchiness on the number and location of dispersal routes. Landscapes become "patchier" as ß values increase. (A) Artificially-generated relative cost grids, (B) CMTC grids, (C) location of MSPs.

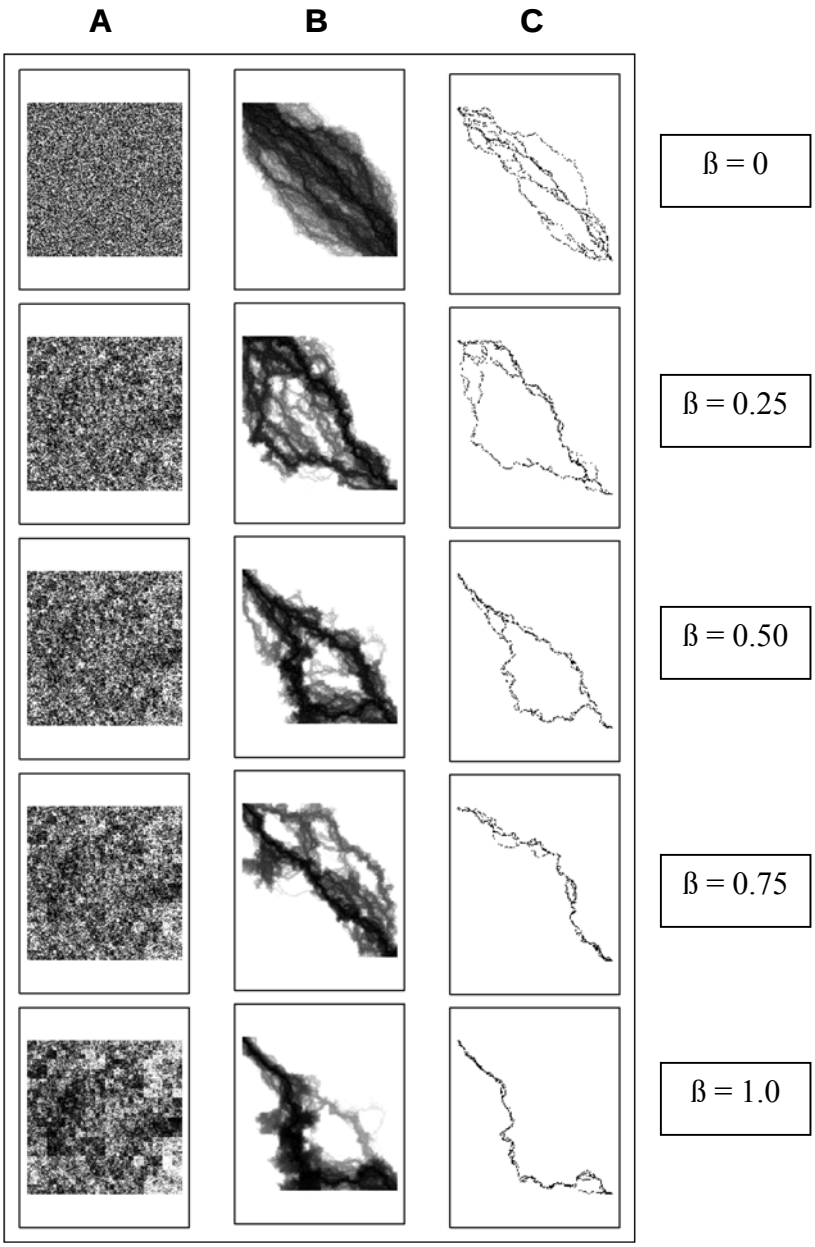
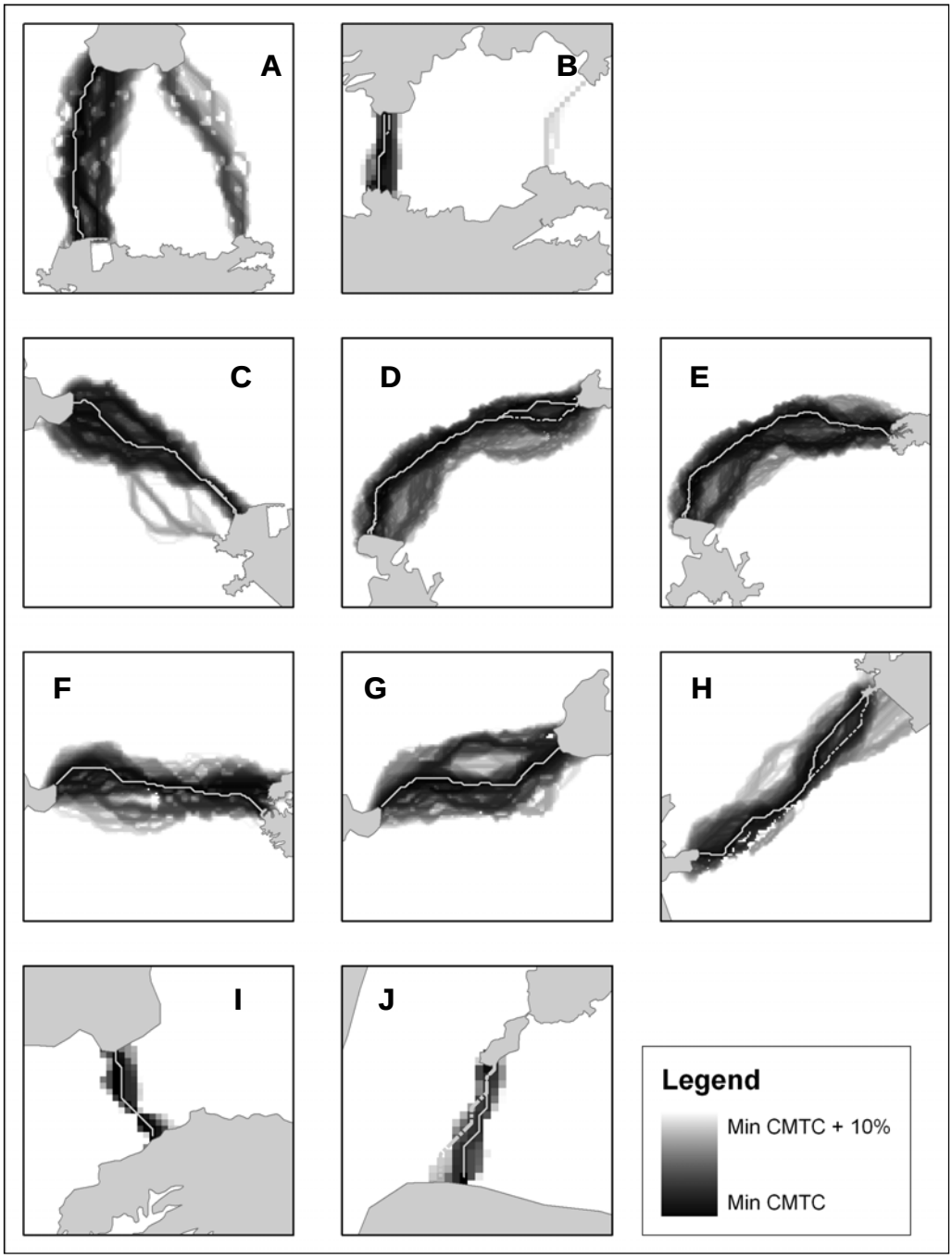


Figure 3-6: CMTC grids for the corridor connecting conservation units in São Paulo, Brazil.



The pairs are: (A) Jurupara-Juréia, (B) Jureia-Serra do Mar, (C) Juréia-Paranapiacaba, (D) Jacupiranga-Jurupará, (E) Jacupiranga-Serra do Mar, (F)

Paranapiacaba-Serra do Mar, (G) Paranapiacaba-Jurupará, (H) Juréia-Jacupiranga, (I) Serra do Mar-Jurupará, (J) Paranapiacaba-Jacupiranga. Gray lines show the least-cost path. Solid lines represent least-cost paths obtained for scenarios C1 and C2, whereas interrupted lines represent sections of the least-cost path obtained for scenario C2 only.

Figure 3-7: Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. (A) Jacupiranga-Serra do Mar, scenario C1; (B) Jacupiranga-Serra do Mar, scenario C2; (C) Juréia-Paranapiacaba, scenario C1; (D) Juréia-Paranapiacaba, scenario C2; (E) Serra do Mar-Paranapiacaba, scenario C1; (F) Serra do Mar-Paranapiacaba, scenario C2.

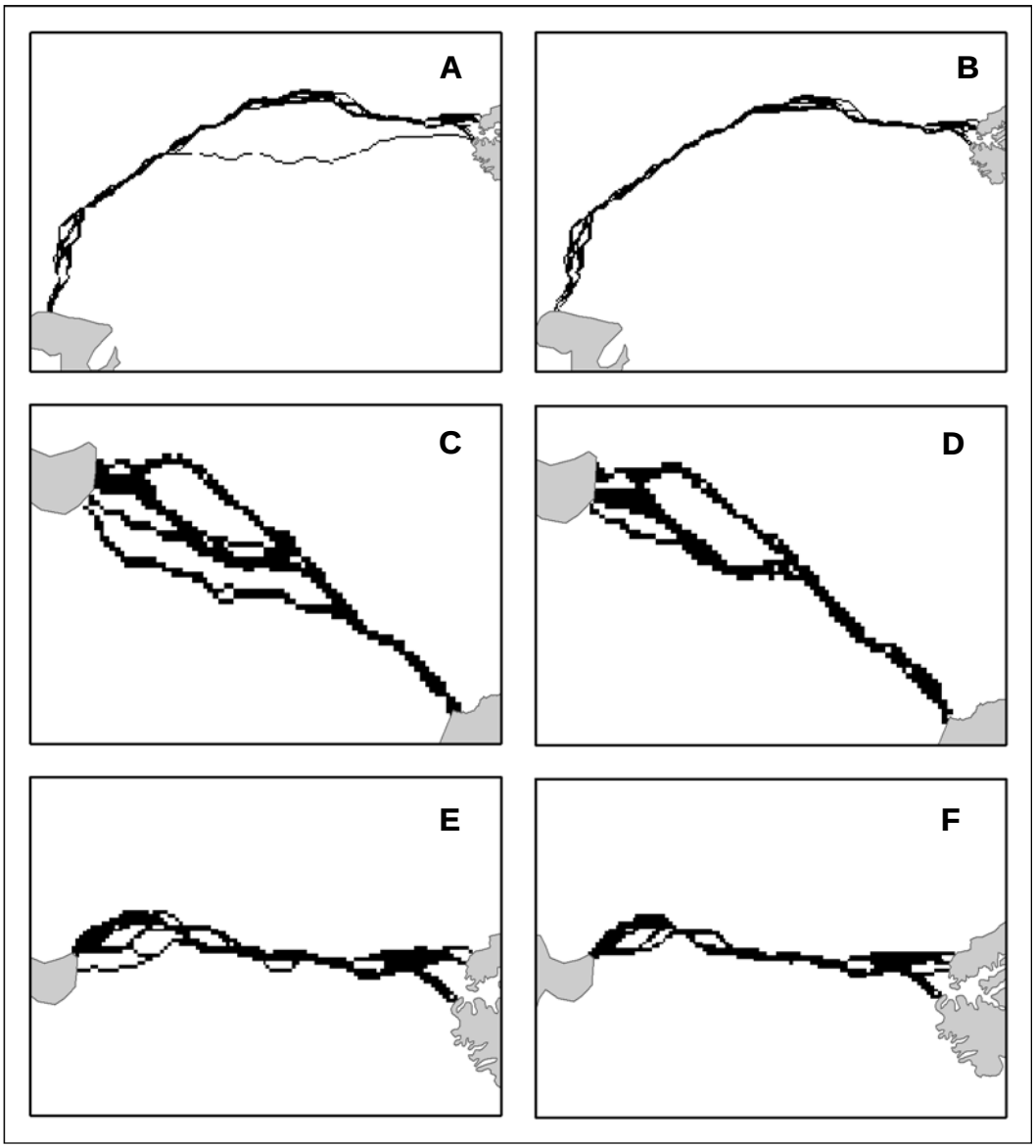
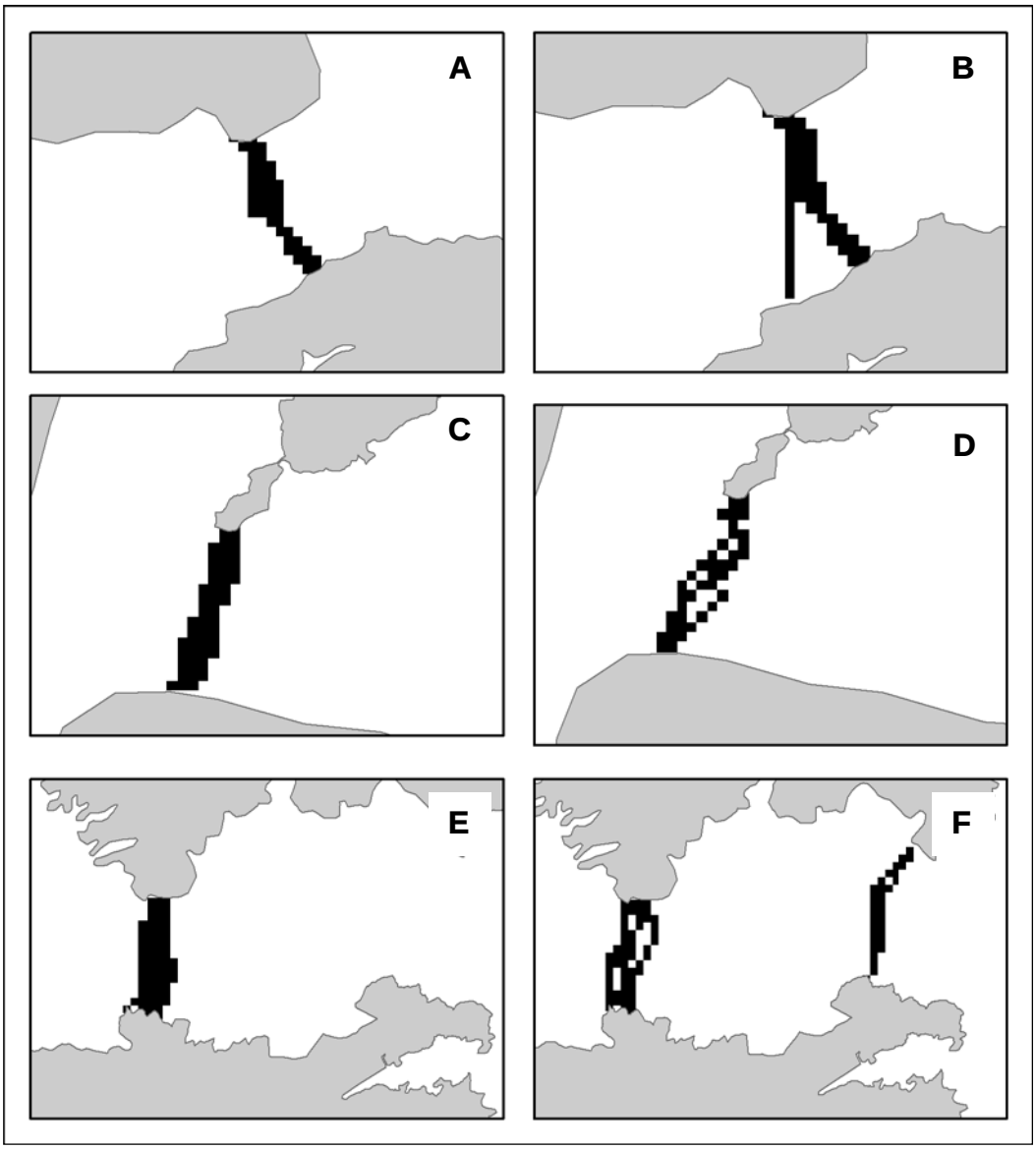


Figure 3-8: Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. (A) Serra do Mar-Jurupará, scenario C1; (B) Serra do Mar-Jurupará, scenario C2; (C) Paranapiacaba-Jacupiranga, scenario C1; (D) Paranapiacaba-Jacupiranga, scenario C2; (E) Juréia-Serra do Mar, scenario C1; (F) Juréia-Serra do Mar, scenario C2.



Finally, we identified the Multiple Shortest Paths (MSPs) between pairs of conservation units. Compared to the CMTC calculation, this tool provided a better assessment of the impact of fragment removal on corridor redundancy. Examining the MSPs produced for the scenarios C1 and C2, we observed two trends. In some cases, fragment removal lead to the disappearance of external dispersal routes; corridors became narrower and less redundant (Figure 3-7). In other cases, new, more external routes emerged after fragment removal (Figure 3-8). However in all cases, we did not detect significant changes in the length or cost (Table 3-3) of the mean least-cost paths linking conservation units.

Table 3-3: Mean and variance of the cost of least-cost path linking conservation units (divided by 1000), calculated using the Multiple Shortest Paths (MSPs) tool. For each pair, the top row shows results calculated before fragment deletion (scenario C1), and the bottom row shows results obtained after fragment deletion (scenario C2).

Juréia	Jacupiranga	Jurupará	Serra do Mar	Paranapiacaba
Juréia	6.9 ± 40.1	3.6 ± 21.3	0.78 ± 4.5	3.7 ± 21.9
	6.8 ± 40.1	3.6 ± 21.3	0.78 ± 4.5	3.7 ± 21.9
Jacupiranga		13 ± 76	14 ± 82.1	0.79 ± 4.6
		13 ± 76.2	14 ± 82	0.79 ± 4.6
Jurupará			0.74 ± 4.3	4.2 ± 24.8
			0.74 ± 4.3	4.2 ± 24.8
Serra do Mar				5.2 ± 30.4
				5.2 ± 30.5

DISCUSSION

We have extended the least-cost path approach by applying modifications to Dijkstra's breadth-first search algorithm. Our first goal was to contribute to ecological studies that require estimates of inter-patch dispersal rates, and add confidence intervals to least-cost path estimates (e.g. Table 3-3). Our second goal was to contribute to management initiatives, by identifying structural features of the landscape that are functionally unique (Manning et al. 2006): narrow corridors with few dispersal routes or bottlenecks within corridors (e.g. Figure 3-5).

Artificial landscapes were used to study the influence of matrix heterogeneity on the number and spatial distribution of dispersal routes. Our results show that redundant corridors with many alternative dispersal routes emerge when the distribution of good habitat is random. As patches of favorable habitat start forming, corridors become narrower and less redundant (Figure 3-5). It is important to note that the results shown in Figure 3-5 can illustrate different landscapes, or the same landscape as perceived by different species. These results are relevant because despite the debate about whether corridors should be narrow or wide (reviewed by Chetkiewicz et al. 2006), few studies have attempted to predict how corridors with different characteristics can emerge in the landscape matrix. In addition to studying artificial landscapes, we illustrated our methods using data from a real landscape in the Brazilian Atlantic forest. With the exception of the pair Paranapiacaba-Jurupará that is separated by an artificial dam (Figure 2-6g), potential dispersal routes could not be predicted based on visual inspection of our land use / land cover maps. Rather, large-scale connectivity patterns emerged from local variation in habitat quality (Figures 3-6a-f, h-j).

The importance of corridors in determining the persistence of natural populations has not yet been determined for the Brazilian Atlantic forest. But in general, our results

may be relevant for conservation initiatives that use the least-cost path to design reserve networks. One way to deal with the narrow links generated by the least-cost path is to aggregate additional habitat around this route (e.g. Hoctor et al. 2000). Our results suggest there are at least two alternative solutions: first, one can protect many disjoint routes with costs similar to the least-cost path. Second, one can locate multiple dispersal routes with costs similar to the least-cost path and from this list, select the optimum route based on other desirable characteristics (price of land, presence of good habitat in the surrounding areas, etc.).

The CMTC and the MSP tools produced similar results (Figures 3-6, 3-7, 3-8), however the latter was more useful in detecting the effect of land cover changes on the distribution of individual dispersal routes. In both cases, results will depend on the researcher's choice method to construct the relative cost grid, the threshold CMTC value used to delimit corridor width, and the number of least-cost paths used when calculating MSPs. We have built a relative cost map in an attempt to capture the behavior of species that move in forested areas and suffer higher mortality when crossing disturbed habitat. If this assumption is valid – individuals preferentially disperse in areas resembling their habitat – tools such as the Mahalonobis distance (Farber and Kadmon 2003) can be employed to produce relative cost maps for particular species. Also, the present analyses did not make any assumptions about the temporal scale of dispersal episodes. That is, we were not concerned with the time interval or number of generations that individuals (or populations) took to move between source and target fragments (conservation units). More realistic models can be obtained by adjusting the maximum Euclidian distance allowed between source and target fragments so as to match the maximum distance that can be crossed by a species given a particular time interval (Keitt et al. 1997).

Movement behavior is a key aspect in functional connectivity studies, but detailed data on animal movement remains hard to collect, especially for large spatial scales. In fact, the ability to produce accurate movement models has long been recognized as one of the main challenges of population biology studies (Turchin 1998). There is no consensus on the amount of biological detail that should be used in functional connectivity studies. It has been suggested that movement models ought to increase in complexity in order to capture the behavior of particular species (Goodwin 2003). At the same time, conservation biologists have raised the need for rigorous methods that predict the location of movement routes for many species (Boitani et al. 2007). Clearly a compromise is needed, which requires determining how much simplification can be made before losing predictive power. Least-cost path predictions can be derived for many species, given the ever growing maps of habitat quality produced by ecological niche modeling. Also, rigorous protocols already exist to compare least-cost predictions with field data (Driezen et al. 2007).

Lastly, considerable attention has been given to quantifying the role played by agroecosystems in conservation (i.e., Bestelmeyer and Wiens 1996; Reitsma et al. 2001; Mas and Dietsch 2003). Agricultural lands can help support wild populations by providing critical habitat (Moguel and Toledo 1999) and influencing neighboring fragments, in which case potential outcomes depend on the spatial configuration and degree of mixture with pristine habitat (Perfecto and Vandermeer 2002; Perfecto et al. 2003; Tscharntke et al. 2005). Our work shows that private lands can collectively influence ecological processes occurring at large spatial scales and supports the assertion that small fragments can potentially shape regional patterns of gene flow (Bodin et al. 2005). This raises the necessity to view agricultural lands' contribution to biodiversity in a larger context.

ACKNOWLEDGEMENTS

I would like to thank Tania Pena-Baca, Catherine Behrman, Jesse Lasky, Betsy Reardon, Courtney Abshire, and two anonymous reviewers for help with the manuscript.

LITERATURE CITED

Bestelmeyer BT, Wiens JA (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentinian Chaco. Ecological Applications 6: 1225-1240.

Belisle M (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. Ecology 86: 1988-1995.

Bodin O, et al. (2005) The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. Ecological Applications 16: 440-451.

Boitani L, et al. (2007) Ecological networks as conceptual frameworks or operational tools in conservation. Conservation Biology 21: 1414-1422.

Burel F (1996) Hedgerows and their role in agricultural landscapes. Reviews in Plant Sciences 15: 169-190.

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and Environment 2: 529-536.

Chardon JP, et al. (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (*Parge aegeria* L.). Landscape Ecology 18: 561-573.

Chetkiewicz CLB, et al. (2006) Corridors for conservation: integrating pattern and process. Annual Review of Ecology and Systematics 37: 317-342.

Clevenger AP, et al. (2001) Drainage culverts as habitat linkages and factors affecting passage by mammals. Journal of Applied Ecology 38: 1340-1349.

Cormen TH, et al. (2001) Introduction to Algorithms. MIT Press, Cambridge, Massachusetts.

Driezen K, et al. (2007) Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). Ecological Modelling 209: 314-322.

Eva HD, et al. (2002) A vegetation map of South America. EUR 20159, European Commission, Joint Research Center.

Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecological Modelling 160: 115-130.

Goodwin BJ (2003). Is landscape connectivity a dependent of independent variable? Landscape ecology 18: 687-699.

Hansen MR, et al. (2003) Vegetation Continuous Fields, MOD44B, 2001 percent tree cover, collection 3. University of Maryland, College Park, Maryland.

Hoctor TS, et al. (2000) Identifying a linked reserve system using a regional landscape approach: the Florida ecological network. Conservation Biology 14: 984-1000.

IBGE (1991) Census of Brazilian municipalities. Available from http:// www.ibge.gov.br

Keitt TH, et al. (1997) Detecting critical scales in fragmented landscapes. Conservation Ecology [online] 1: 4. Available from the internet: URL: http://www.consecol.org/vol1/iss1/art4

Larkin JL, et al. (2004) Landscape linkage and conservation planning for the black bear in west-central Florida. Animal Conservation 7: 23-34.

Laurance WF, et al. (2002) Ecosystem decay of forest fragments: a 22-year investigation. Conservation Biology 16: 605-618.

Lees AC, Peres CA (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conservation Biology *in press*.

Mallat, SG (1989) A theory for multiresolution signal decomposition: the wavelet representation. IEEE Transactions on Pattern Analysis and Machine Intelligence 11: 674-693.

Manning AD, et al. (2006) Scattered trees as keystone structures – implications for conservation. Biological Conservation 132: 311-321.

Mas AH, Dietsch TV (2003) An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. Ecological Applications 13: 1491-1501.

Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13: 11-21.

Morellato LPC, Haddad CFB (2000) Introduction: the Brazilian Atlantic forest. Biotropica 32: 786-792.

Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica 32: 793-810.

Perfecto I, et al. (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation 12: 1239-1252.

Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conservation Biology 16: 174-182.

Reitsma R, et al. (2001) The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. Agroforestry Systems 53: 185-193.

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158: 87-99.

Sanderson EW et al. (2002) The human footprint and the last of the wild. Bioscience 52: 891-904.

Schadt S, et al. (2002) Rule-based assessment of suitable habitat and patch connectivity for Eurasian Lynx in Germany. Ecological Applications 12: 1469-1483.

Sutcliffe OL, et al. (2003) Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landscape and Urban Planning 63: 15-31.

Stevens VM, et al. (2006) Gene flow and functional connectivity in the Natterjack toad (*Bufo calamita*). Molecular Ecology 15: 2333-2344.

Tscharntke T, et al. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8: 857-874.

Turchin P (1998) Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Sinauer Associates, Massachusetts, USA.

Urban DL, Keitt TH (2001) Landscape connectedness: a graph theoretic perspective. Ecology 82: 1205-1218.

Vandermeer J, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. American Naturalist 158: 211-220.

Verbeylen G, et al. (2003) Does matrix resistance influence Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? Landscape Ecology 18: 791-805.

Chapter 4: Primate Densities in the Atlantic Forest of Southeast Brazil: The Role of Habitat Quality and Anthropogenic Disturbance

ABSTRACT

In the present work, we focused on southeast Brazil's Atlantic forest and studied five primate genera: *Alouatta*, *Brachyteles*, *Callithrix*, *Callicebus*, and *Cebus.* After data were compiled from census studies that used the line transect method, we applied regression trees in order to search for determinants of variation in primate density. Owing to its location in Brazil's most developed region, the Atlantic forest is not only highly fragmented, but also embedded in a landscape matrix encompassing a wide range of land use types and social contexts. Thus, the independent variables used in the regression analyses included not only surrogates of forest type (e.g., climate) and fragment size, but also data on social indicators and estimates of accessibility derived from human movement models. For all genera, we found that density was strongly influenced by forest type, and not influenced by our accessibility estimates. Interestingly, genera differed in their responses to land use and social indicators, a result that emphasizes the importance of incorporating information on the landscape matrix when performing habitat suitability analyses. The regression models produced here were used to construct maps of predicted primate density for the Brazilian southeast. Overall, the maps for all genera showed high predicted primate densities for the inland semideciduous forests, where primary productivity is expected to be higher. Finally, we suggest that more synthetic work is needed in our study area, and list a few topics in need of research.

INTRODUCTION

Goals

Studies of variation in abundance within a species' geographic range provide the connection between the disciplines of ecology and biogeography. Empirical studies of various taxonomic groups show that density for a given species is unevenly distributed in space, with few "hotspots" and many "coldspots", where abundance is orders of magnitude lower (Brown et al. 1995). The typical explanation for this pattern is spatial variation in habitat suitability. In other words, variation in density is generated by how closely sites correspond to a species' niche (Brown et al. 1995). The correspondence between primate density and habitat suitability can be investigated at several spatial scales (Wiens 1989; Levin 1992). For example, coarse-scale studies comparing densities of howler monkeys (*Alouatta* spp.) across the Neotropics have shown that howler density is largely a function of primary productivity (Peres 1997). Fine-scale studies comparing neighboring forest fragments have also reported variation in howler density, but in this case the pattern is frequently attributed to anthropogenic pressure (Hirsh et al. 1994; Cullen et al. 2001; Chiarello 2003; Martins 2005).

In general, human impact on other primates can be direct via hunting, or indirect through habitat disturbance and fragmentation. But some species thrive in disturbed habitats (Chiarello 1993, 2003; Rylands et al. 1993; Strier 2000), which complicates the task of predicting changes in primate density across a gradient in land use. In the present chapter, we investigate the synergistic effects of environmental and anthropogenic factors on the density of five primate genera that inhabit the Atlantic forest of southeast Brazil. Our goal is not to produce distribution maps, but rather to: (i) synthesize available census information for the region; (ii) compare the genera's responses to anthropogenic impact; and (iii) map areas of high predicted densities based on available data. In this section, we

introduce the reader to the Brazilian Atlantic forest, present the dataset used in the study, and describe the analytical tools used to study the determinants of primate density.

The Primates at the Brazilian Atlantic Forest

Studies in the Brazilian Atlantic forest provide an ideal opportunity to understand the interaction of direct anthropogenic factors and habitat quality on primate densities. This ecosystem is a biodiversity hotspot that occupies less than 8% of its original extent (Hirota 2003). Current studies estimate that 40% of the tree and shrub species in this ecosystem are endemic, as well as 22% of their bird and mammal species (Brooks et al. 2000) – and many new species are still being discovered in the region every year (Alves et al. 2006; Donha and Eliasaro 2006; Pontes et al. 2006). Due to its extensive elevational and latitudinal ranges, the Atlantic forest is recognized as a domain that includes several vegetation types (Oliveira-Filho and Fontes 2000). Exploitation of Atlantic forest species did not start recently, as it has been suggested that hunting and forest clearing were already widespread when the first Portuguese arrived in 1500 (Dean 1996). However, the anthropogenic pressure was intensified with the Portuguese colonization, expansion of the agricultural frontier (Dean 1996; Câmara 2003), and later establishment of Brazilian industrial centers in the area, which currently has a population of more than 130 million people (IBGE 2000). As a result of the intense land use in eastern Brazil, the distribution of forest remnants is very distinct from the fishbone pattern observed in the Brazilian Amazon, in which vast forest tracts are interrupted by a network of roads and pipelines. Rather, the Atlantic forest landscape is now an archipelago with small forest fragments embedded in a human-dominated matrix containing pastures, plantations, cities, and roads.

Twenty-four primate species are known to live in the Brazilian Atlantic forest, twenty of which are endemic to this ecosystem (Hirsh et al. 2006). According to the most recent IUCN Mammal Red List (IUCN 2006), three species are vulnerable, four are endangered and eight are critically endangered (Table 3-1). While some primate populations in the Brazilian Amazon may be sustained via source-sink dynamics (Michalski and Peres 2005), these dynamics have never been documented for the Atlantic forest and are unlikely to be operating due to inter-fragment isolation and inhospitality of the matrix. Also, few fragments are large enough to sustain viable primate populations (Chiarello and Melo 2001; Bernardo and Galetti 2004; see also Marsden et al. 2005 for birds), and the extent to which existing conservation units are protecting primate populations against poaching remains unknown.

Data for Primate Species in the Brazilian Atlantic Forest

Data on primate abundance were compiled from a variety of sources including graduate theses, primary-literature publications, and grey-literature reports. In all cases, data were collected using line transect technique (Buckland et al. 2001). Values of population sizes were often calculated assuming no spatial variation in density within sites. Since this assumption is rarely met, we only show the number of viable populations (>500 individuals estimated) instead of attempting to calculate exact population sizes (Table 4-1).

There are a number of limitations inherent in the type of data used in this study. First, line-transect census data are available for only eleven of the twenty-four primate species that inhabit this ecosystem. Also, studies are mostly restricted to the states of Sao Paulo, Espirito Santo and Minas Gerais (Figure 4-1), and intensive census studies are lacking for populations inhabiting states such as Parana, Santa Catarina, and northeast

Brazil, where few forest fragments remain and some primate populations are believed to be on the brink of extinction, especially large-bodied species (Pontes et al. 2006).

Figure 4-1: Location of primate census studies carried out in the Brazilian Atlantic forest. The statistical analyses presented here focus on the southeast region, composed of the states of Minas Gerais, São Paulo, Rio de Janeiro, and Espírito Santo.

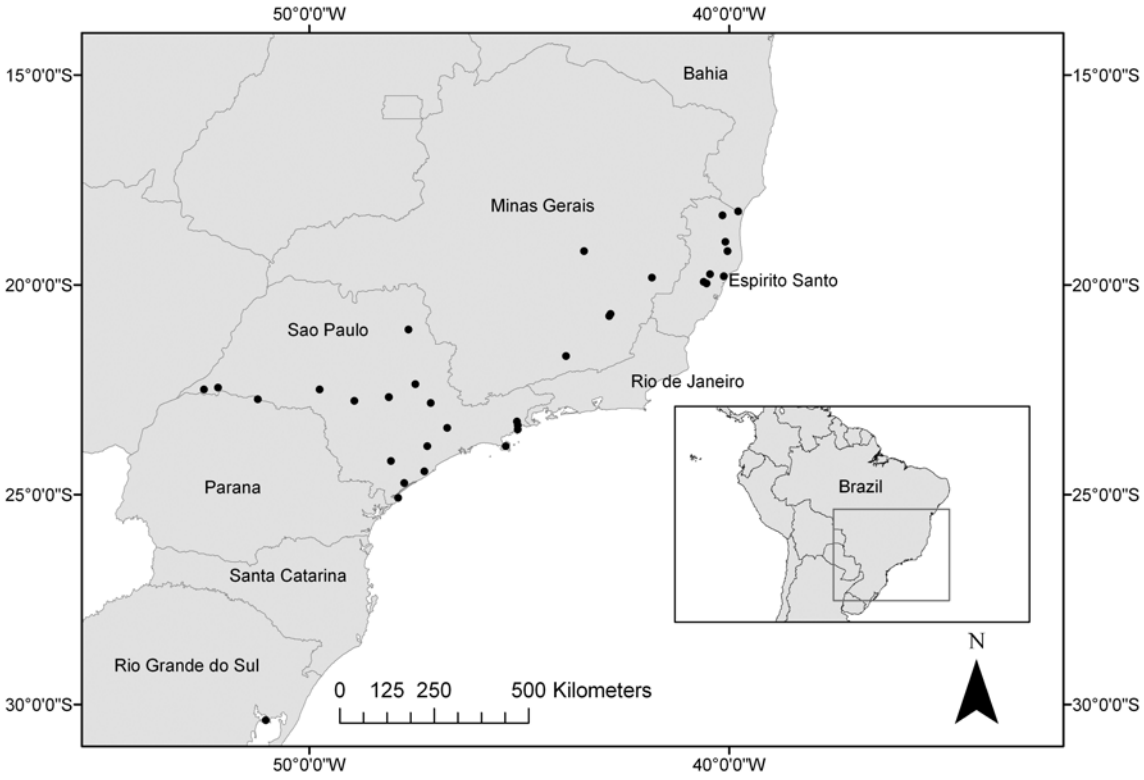


Table 4-1: Primate species inhabiting the Brazilian Atlantic forest, their conservation (IUCN) status, number of sites that have been censused using the line-transect technique, and number of populations with 500 individuals or more. CE = Critically endangered, E = Endangered, V = Vulnerable. See Appendix I for references. * Recently described species (1 population).

Species	Status	Census Sites	≥ 500
Alouatta clamitans	CE	24	8
Alouatta belzebul	CE	0	-
Brachyteles arachnoides	E	9	3
Brachyteles hypoxanthus	CE	2	0
Callicebus barbarabrownae	CE	0	-
Callicebus coimbrai	CE	0	-
Callicebus melanochir	V	0	-
Callicebus nigrifons	-	3	1
Callicebus personatus	V	8	5
Callithrix aurita	V	4	1
Callithrix flaviceps	E	2	1
Callithrix penicillata	-	2	1
Callithrix geoffoyi	-	5	2
Callithrix jacchus	-	0	-
Callithrix kuhlil †	-	0	-
Cebus queirozi	-*	0	-
Cebus libidinosus	-	0	-
Cebus nigritus	-	25	10
Cebus xanthosternos	CE	0	-
Leontopithecus caissara	CE	0	-
Leontopithecus chrysomelas	E	0	-
Leotopithecus chrysopygus	CE	5	1
Leotopithecus *rosalia*	E	0	-

Tools Used in the Present Study

Our task faces two challenges in addition to data scarcity and non-homogeneous sampling across the ecosystem: first, dealing with non-linear relationships and correlations between the independent variables, and second, the fact that the influence of a given environmental correlate can manifest itself at unknown spatial scales – for example, it is not possible to determine beforehand the area of influence of a city and therefore its potential impact on neighboring forest fragments. In the present chapter, we will apply tools that can help deal with the difficulties cited above: geographic information systems (GIS) and regression trees.

The Use of GIS in Conservation Studies

The use of remote sensing and GIS has recently increased among biologists, because these tools facilitate the analysis of large-scale associations between landscape patterns and biological outcomes. In the present work, three classes of maps are employed to model primate densities. First, maps of climate and elevation are used to differentiate between the evergreen coastal rainforest and the semideciduous forest (Oliveira-Filho and Fontes 2000). This distinction is extremely relevant for folivorous species (Peres 1997), because leaves from perennial trees are expected to be tougher (Coley 1983) and have lower nutritional content (Aerts 1996) than leaves from deciduous trees. Second, we used maps of human accessibility, land use, and social indicators, which can potentially serve as surrogates of anthropogenic disturbance and hunting pressure (Siren et al. 2006; Brashares et al. 2001; Laurance et al. 2005). Third, we used maps of fragment size. Note that climate and elevation maps reflect local habitat quality, whereas the other maps are based on information from the neighboring municipalities and road network that surround study sites.

Regression Trees

The statistical analysis of the relationship between environmental factors and population sizes is complicated by the existence of interactions (often non-linear) among environmental predictors. For example, forest type is known to correlate with temperature, precipitation and elevation (Oliveira-Filho and Fontes 2000). Moreover, the exact shape of these relationships is unknown. Thus, we decided to use a data mining approach that enables us to look for environmental determinants of primate density while accommodating for non-linear interactions between predictors and which does not require the specification of the relationship between the response and the predictors. Here, we will use Random Forest, a tree regression method (Breiman 2001; Liaw and Wiener 2002). This method recently started being applied in several areas of biology involving data mining, such as bioinformatics (Pang et al. 2006) and niche modeling (Garzon et al. 2006; Prasad et al. 2006). The algorithm works by iteratively splitting the group of data points. Each tree node represents a splitting rule (e.g., "elevation > 1500 m"), and nodes are followed by two branches representing the newly separated data points. More specifically, the splits are performed using the predictor variables to partition the response variable into two groups, so as to maximize the between-groups sum of squares. The output tree contains a series of branches representing the optimized sequence of splitting rules. Random Forest grows hundreds of trees, each one using a subset of the independent variables. The resulting trees are then averaged to obtain the final model, a procedure that reduces overfitting (Breiman 2001). As in other niche model and classification tools, data points are partitioned into a training set, used to construct the model, and a testing set, used to access model accuracy. For a very accessible review of regression tree methods, see Berk (2006).

METHODS AND ANALYSES

Study Area

The study area comprises four Brazilian states: São Paulo, Rio de Janeiro, Minas Gerais and Espírito Santo (Figure 4-1). The region spans the two main Atlantic forest domains: the Atlantic rainforest and the Atlantic semideciduous forest. The former comprises areas up to 300 km inland that have high annual precipitation due to oceanic winds and mountain ranges, whereas the latter includes plateau areas with higher elevation and lower annual precipitation. For a detailed description of the forest types, see Oliveira-Filho and Fontes (2000).

Target Genera

We focus on five genera: (1) *Brachyteles* (muriqui), the largest species at 12 kg, a frugivore-folivore (Milton 1984; Strier 1991) that is distributed along the Brazilian southern states of São Paulo, Rio de Janeiro, Espírito Santo, and Minas Gerais, and the states of Paraná and Bahia; (2) *Alouatta* (howler monkey), a folivore (Glander 1978; Mendes 1989; Peres 1997) weighing 6.4 kg, distributed in the Brazilian south and all the way to the northeast along the coast; (3) *Cebus* (capuchin monkey), an insectivore-frugivore (Fragaszy et al. 2004) weighing 2.5 kg inhabiting the entire country except the extreme south; (4) *Callicebus* (titi monkey), a folivore-frugivore (Price and Piedade 2001) weighing 1.35 kg inhabiting the Brazilian southeast, northeast and Amazon; and (5) *Callithrix* (marmoset), the smallest species at 0.30 Kg. Neotropical marmosets feed on a large range of plant materials, including gums, fruits, and seeds, as well as animal preys (Correa et al. 2000). They are distributed along the Brazilian southeast, northeast and Amazon.

Compilation of Census Data

We compiled a list of census studies carried out between the years of 1993 and 2005 (Fig. 4-1; Appendix I). In order to make the data comparable, we selected studies that used the line-transect technique (Buckland et al. 2001). This method basically consists of establishing transects distributed randomly or stratified according to habitat type and counting the number of individuals encountered. Information on straight-line distance to observed individuals is used to calculate the effective strip width (ESW) and estimate local density. Line transect is considered one of the most precise census techniques and due to its simplicity and cost-effectiveness, it has been applied to census a broad range of animal and plant populations (Buckland et al. 2001). A total of 17 census studies using line-transect technique were found, and 16 were carried out within the Brazilian southeast. Out of those 16 studies, four were excluded: one study reported large within-site variation but did not provide separate density values for those sites (Hirsh et al. 1994); a second study was performed in a field site for which more recent information was available (Pinto et al. 1993); a third dataset (Chiarello 1993) reported extremely high density values for *Alouatta* in an urban park in Sao Paulo State. Preliminary models using this data point predict that all urban centers will have the highest howler densities. Although it is our intention to predict the impact of urbanization on primate densities, we believe that the conditions leading to the density value observed by Chiarello (1993) are probably tied to historical factors and latent variables that we are presently unable to measure. Last, we excluded data from Anchieta Island (Bovendorp and Galetti 2007) because this island has been a target of "repopulation" initiatives and several vertebrate species have been recently introduced in the area.

GIS

For each primate genus, we obtained a grid map containing values for the dependent variable to be used in the tree regression, primate density (individuals / km^2). In order to locate study sites for which density information was available, we used a map of percent tree cover (Modis Vegetation Continuous Fields, Hansen et al. 2003), a forest inventory available for Sao Paulo state only (BIOTA-Fapesp), and the figures available in the original publications. For large parks in São Paulo state, we used the location of transects buffered by a distance of 500 m. Data were pooled for small, contiguous fragments. Those fragments are (1) Sao Lourenço, Santa Lucia and Augusto Ruschi, and (2) M7 and Putiri, all of them in Espírito Santo state (see Chiarello 2003). In these cases, primate densities were averaged across fragments.

In addition, we obtained 12 grid maps representing the independent variables to be used in the tree regression (Table 4-2). Two grid maps are derived from least-cost path estimates used to model human movement across the landscape. The first one contains, for each cell, the number of people that can reach that cell when traveling by road for a maximum of 30 minutes. This was based on human census data for each municipality and a road network map. The model was built using the module Network Analyst within ArcGIS (ESRI, California). We assumed people departed city centroids and traveled along federal and state highways at a speed of 100 km/hour. Since location of city streets and dirt roads was not available, it was assumed individuals leaving highways would travel to their final destinations along a straight line, at 50 km/hour. A second grid map represents human accessibility, assuming people are moving by foot. The map contains the relative cost to reach each cell from the nearest city, assuming that cost is a function of distance and slope.

Table 4-2: List of GIS layers containing the independent variables used in the tree regression analysis.

Variable Name	Code	Units	Original Resolution (m)	Year(s) Data Collected	Ref
Percent tree cover	perctree	%	500	2001	1
Mean annual temperature	mean_temp	Celsius * 10	800	1950 - 2000	2
Temperature seasonality	var_temp	SD * 100	800	1950 - 2000	2
Total annual precipitation	precip	mm	800	1950 - 2000	2
Precipitation seasonality	var_precip	Coefficient of variation	800	1950 - 2000	2
Elevation	elevation	Meters	1000	various	3
Slope-based accessibility	cost_slope	Relative cost	1000	1996 (cities) and various (elevation)	3, 4
Road-based accessibility	access	Number of people / 100,000	5000	1996 (census) and 2001 (roads)	4, 5
Industry	industry	Number of units	Per city	1996	4
Crop area	crop	Percent area devoted to permanent agriculture plots	Per city	1995	4
Median income	income	Median income for all people older than 10, in Reais	Per city	2000	4
Fragment size	size	Unitless (size classes from 1 to 6)	20	1999 - 2000	6

Hansen et al. 2003; (2) Hijmans et al. 2005; (3) Danko 1992; (4) IBGE 1996; (5) DNIT 2001; (6) Eva et al. 2002.

Although urban centers are obviously served by a large concentration of roads, some agricultural areas are also located near highways. In order to distinguish between these two land use types, we produced maps containing values of area devoted to agriculture, as well as degree of industrialization. In addition, a map of median income for each municipality (IBGE 1996) was produced in an attempt to obtain a surrogate for anthropogenic disturbance and/or hunting pressure. Last, forest fragments were mapped using a global land cover database (Eva et al. 2002). After excluding areas classified as "mosaic agriculture/degraded forest", the area for each fragment was calculated. We then assigned each cell with a value representing the size, in hectares, of the fragment where the cell is located. Six classes were used: (1) < 100; (2) > 100 and < 316; (3) >316 and < 1000; (4) >1000 and < 3162; (5) > 3162 and < 159,000; (6) > 159,000. All maps were re-scaled to 500-m resolution. All GIS analyses were performed using ArcGIS 9.2 (ESRI, California). Map layers can be made available upon request to the first author.

Random Forest

The parameters used in the Random Forest run were: 3 independent variables (Table 4-2) could be used at each split; sampling was stratified, in such a way that all study areas are used to grow each tree; 500 trees were grown. After the run, we computed the variable importance for all independent variables. This is estimated in two ways: mean percent increment in square error, which is the average increase in prediction error when a given predictor is shuffled, and percent increase in node impurity, which is the within-node variation (residual sum of squares) obtained when the variable is shuffled (Breiman 2001; Prasad et al. 2006). Also, partial plots were constructed to study the relationship between the four most important environmental correlate and primate density. These plots are built by computing the relationship between the target predictor

and the response averaged over the joint values of the other variables (Berk 2006). Last, the models were used with the entire range of values in the Brazilian southeast in order to predict density values for this region. All statistical analyses were performed in R (R Development Core Team 2007).

RESULTS

General Aspects

When analyzing data for individual genera, we found no significant relationship between sampling effort (number of kilometers sampled) and density for *Alouatta* ($p = 0.76$), *Brachyteles* ($p = 0.47$), *Callicebus* ($p = 0.59$), *Cebus* ($p = 0.08$) or *Callithrix* ($p = 0.85$). If absences are removed, there is a significant relationship between log-transformed proportional sampling effort (number of kilometers sampled / area of study site) and log-transformed density for *Alouatta* ($p < 0.001$; $Density = 0.68 + 0.61 * Sampling\ effort$; $R^2 = 0.36$) but not for the remaining species (*Brachyteles*, $p = 0.14$; *Cebus*, $p = 0.76$; *Callicebus*, $p = 0.25$; *Callithrix*, $p = 0.69$).

For all genera, most sites are "coldspots" with lower densities and few sites are "hotspots". Within-genus variation in density reached three orders of magnitude for some genera: for *Alouatta*, density (individuals / km^2) ranges from 0.29 to 176.80 (mean ± SD: 23 ± 38, N = 20). For *Brachyteles*, density ranges from 0.42 to 35.11 (9.63 ± 11.6, N = 10). Density values for the genus *Cebus* range from 0.90 to 49.88 (16.63 ± 15.25, N = 23). For *Callithrix*, density ranges from 1.83 to 110.3 (22.1 ± 29.4, N = 10). Last, density for *Callicebus* ranged from 3.5 to 157 (24 ± 45.34, N = 9). No significant difference was found in among-genera densities (Kruskal-Wallis rank-sum test, $p = 0.09$).

Determinants of Primate Density

A tree regression analysis using Random Forest was performed to study the effect of 12 variables (Table 4-2) on primate density. For all genera, the model was able to explain more than 90% of the variability in the training set. The output models produced by Random Forest were applied to the entire Brazilian southeast region (Figures 4-2, 4-4, 4-5, 4-6). For all genera, the five most important predictors of primate density included precipitation and temperature, although genera responded differently to these climatic variables (Table 4-3). The five genera also displayed different responses to land use. For example, an increase in the area devoted to agriculture had a positive impact on the densities of *Callicebus spp.*, but a negative impact on *Alouatta spp.*; also *Cebus spp.* displayed higher densities in the vicinity of industrialized cities (Table 4-3). In most cases, partial plots showed a simple negative or positive influence of the independent variables on densities (shown as "+" or "-" on Table 4-3), but sometimes densities peaked at intermediate conditions (in this case, actual values are shown on Table 4-3). For example, density for *Callithrix spp.* was highest at intermediate values of median income and temperature (Table 4-3).

Table 4-3: List of the five most important determinants of primate density for five primate genera. See Table 3-2 for variable codes.

Variable	*Brachyteles*	*Alouatta*	*Callicebus*	*Cebus*	*Callithrix*
perc_tree			-		
cost_slope	-				
mean_temp		20 ºC	-		24 ºC
var_temp	+			+	-
var_precip	+	+		+	
precip		-	+	1400 to 1800 mm	1200 mm
elevation	-			-	-
income	+		-		200 to 300 Reais
industry				+	
crop		-	+		
size		3162 to 159,000 ha			

Figure 4-2: Map of predicted densities of muriquis (*Brachyteles* spp.) in the Brazilian southeast.

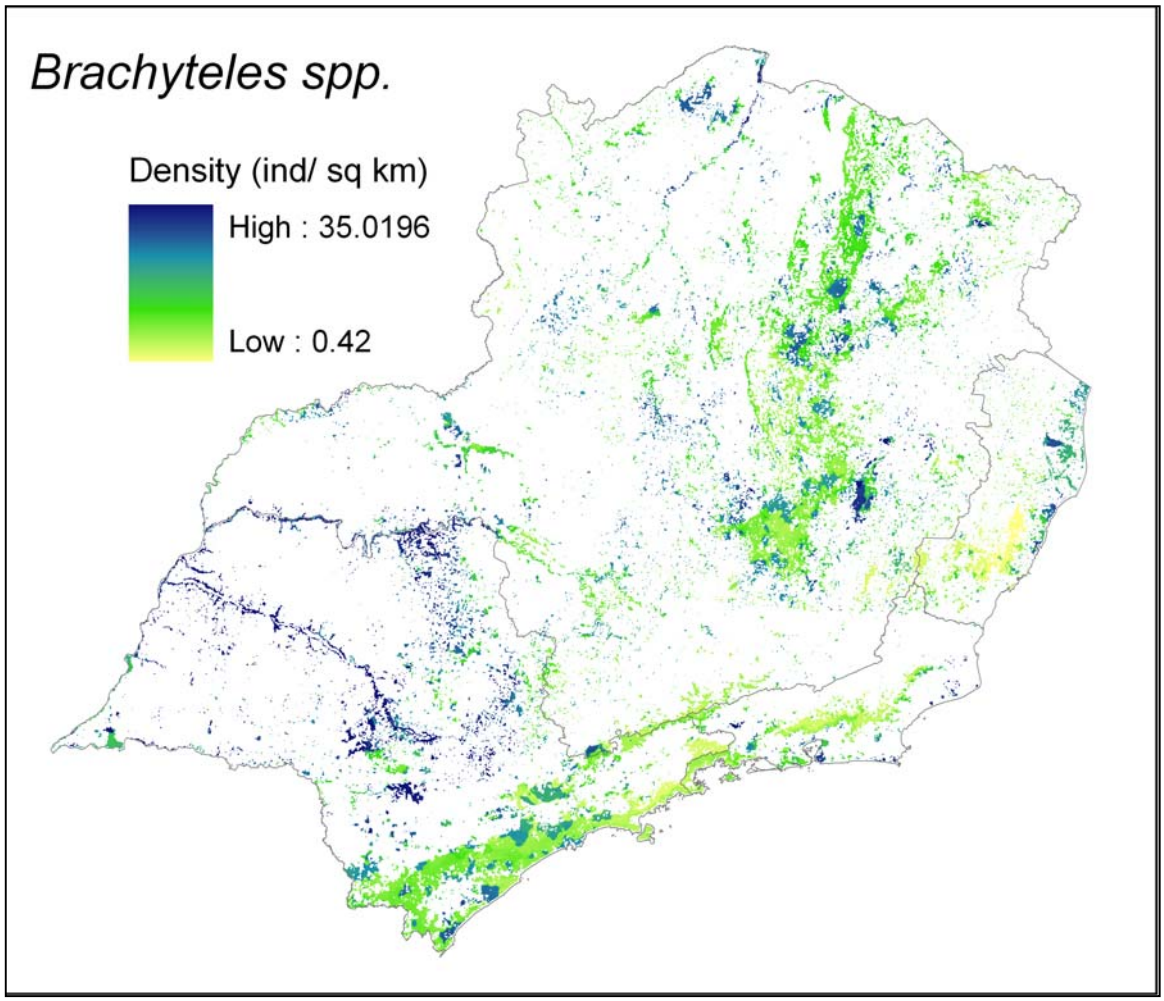


Figure 4-3: Map of predicted densities of howler monkeys (*Alouatta* spp.) in the Brazilian southeast.

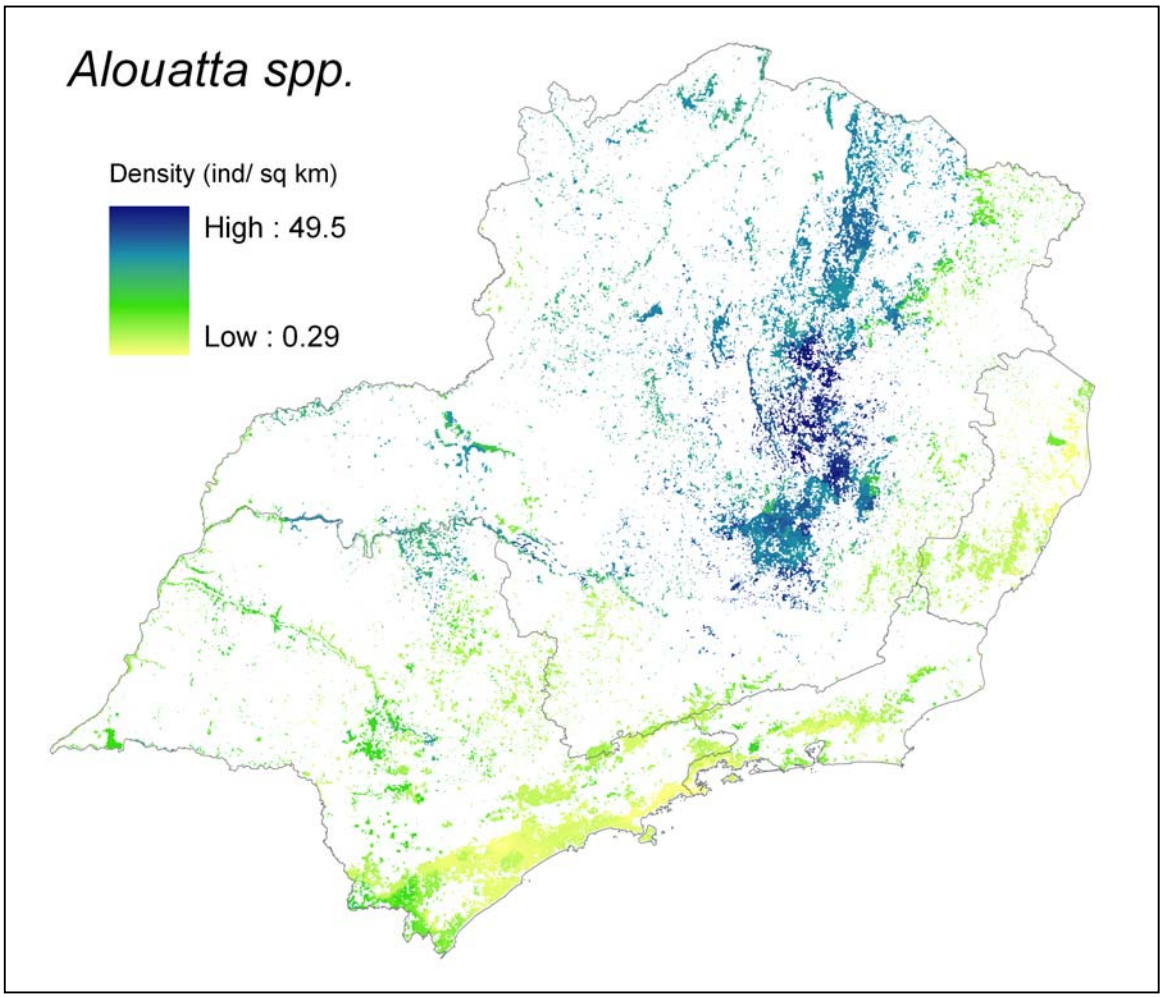


Figure 4-4: Map of predicted densities of capuchin monkeys (*Cebus* spp.) in the Brazilian southeast.

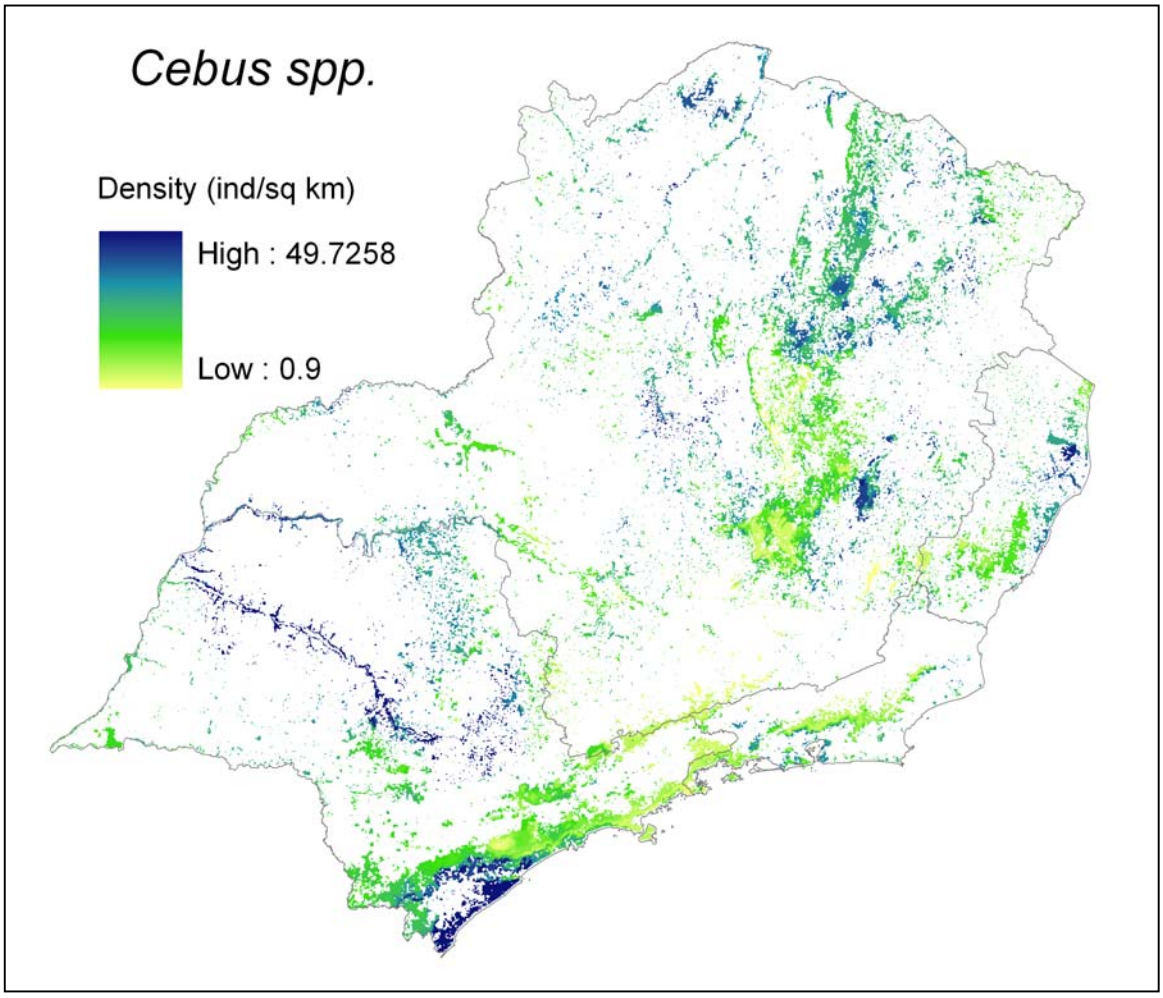


Figure 4-5: Map of predicted densities of titi monkeys (*Callicebus* spp.) in the Brazilian southeast.

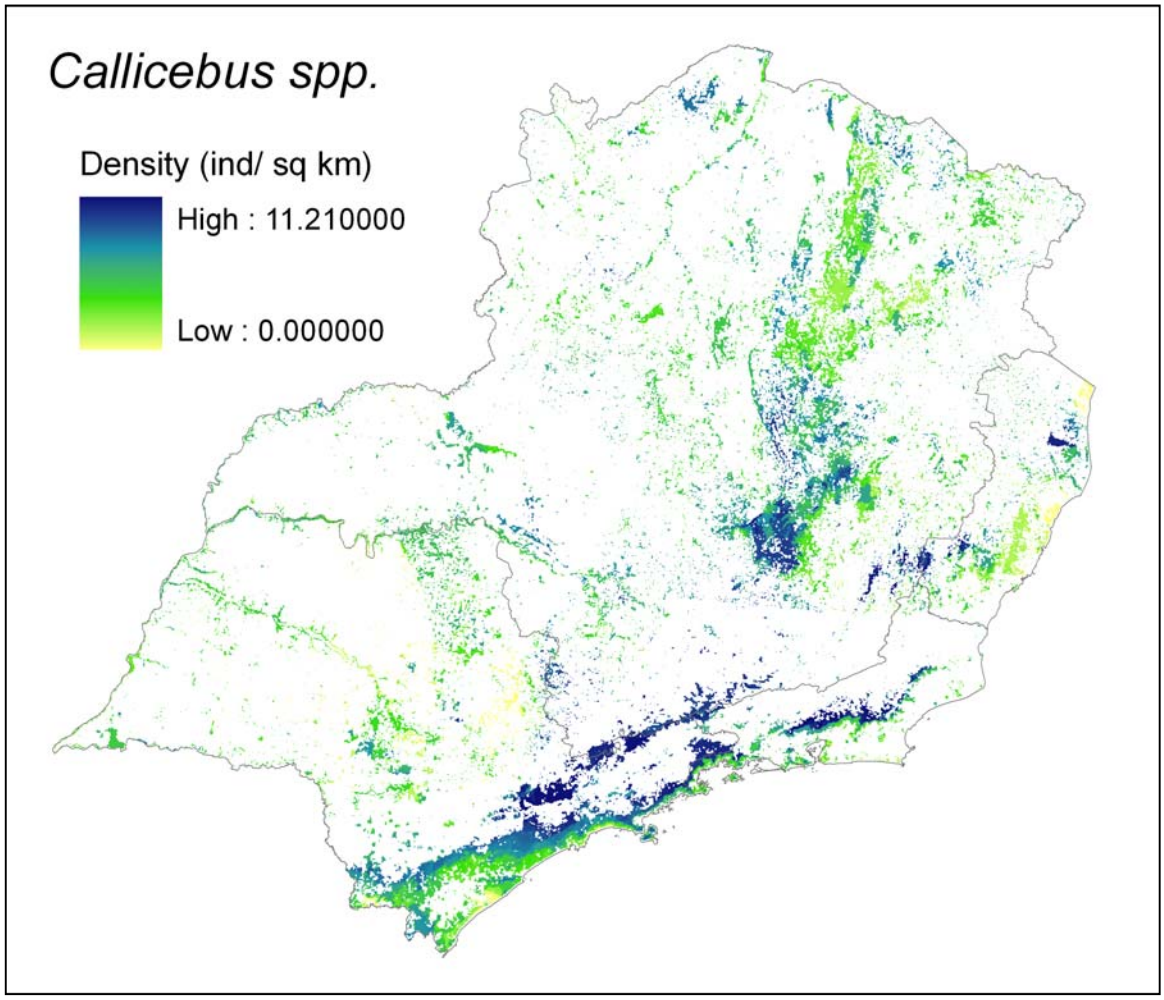
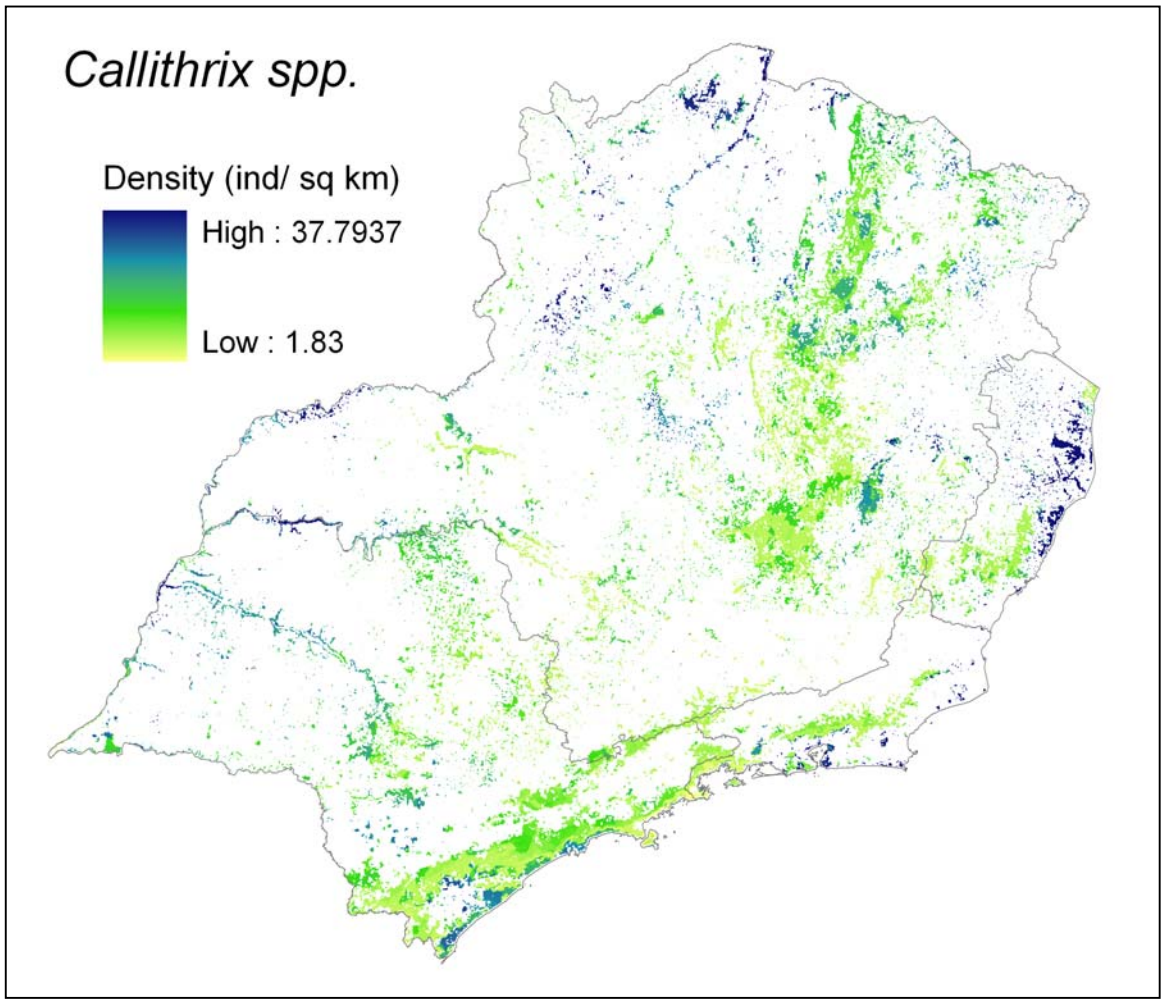


Figure 4-6: Map of predicted densities of marmosets (*Callithrix* spp.) in the Brazilian southeast.



DISCUSSION

Predicted Primate Density Hotspots

The analyses carried out in the present work enable us to tease apart the effects of anthropogenic impact and forest type on densities of primate species inhabiting a highly disturbed ecosystem. For all species, densities decreased with fragment size, although this variable was not always an important predictor of primate density (Table 4-3). Accessibility by road is not an important predictor of density for any of the target genera (Table 4-3). Accessibility by foot was modeled as a function of slope (see Methods) and had a positive impact on *Cebus* spp., *Callithrix* spp. and *Brachyteles* spp. (Table 4-3), that is, areas considered accessible had higher primate densities. This variable is thus probably serving a substitute for slope. Overall, results suggest that patterns of land use and social indicators from municipalities where fragments are located provide better estimates of anthropogenic impact than models of human movement.

For all genera but *Cebus*, areas with non-zero estimated density extended beyond the described distribution for the species used to train the model. There are a few possible reasons that might explain this result. First, there are different accounts on the southern edge of distribution for the genus *Callicebus* (Rylands and Faria 1993; Hirsh et al. 2006). For *Callithrix* spp. and *Alouatta* spp., the Random Forest model probably identified areas in the cerrado (the Brazilian savanna) showing climatic patterns that are similar to the one found in the Atlantic forest. The cerrado ecosystem is inhabited by species that have not been considered in our analyses but that nevertheless belong to the target genera studied here, such as *Callithrix penicillata* and *Alouatta caraya*.

The largest genus, *Brachyteles*, did not display a clear preference for a particular forest type, as densities are predicted to be high in coastal zones as well as inland (Figure 4-2). Predicted hotspots are low, flat rainforest zones in São Paulo State and Espírito

Santo, as well as semideciduous forest in Minas Gerais and west of São Paulo (Figure 4-2). Fragments located in municipalities with low income displayed lower densities (Table 4-3). Income has been demonstrated to correlate with hunting pressure in other ecosystems (Shively 1997), although researchers differ in the procedure used to estimate income (Godoy et al. 2006) and many other factors such as employment stability might also play a large role in people's decision to consume wild meat (Siren et al. 2006). Income might also be correlated with pet trade, but to our knowledge no studies have demonstrated this relation.

The most folivorous genus, *Alouatta*, showed a clear preference for areas with high precipitation seasonality, low annual precipitation, and high temperature seasonality (Table 4-3). Predicted hotspots are thus areas of semideciduous forest in Minas Gerais (Figure 4-3). This is in accordance with recent models developed for the Neotropics as a whole (Peres 1997), which showed that variation in density for *Alouatta* is largely governed by primary productivity. Fragments located in agricultural zones had lower *Alouatta* density, suggesting a negative effect of the landscape matrix that surrounds forest fragments, and/or that inhabitants of rural zones are more likely to engage in hunting activities.

The capuchin monkey (*Cebus* spp.) showed a preference for areas with low elevation, high mean temperatures, high temperature seasonality, and high precipitation seasonality (Table 4-3). Industrialization had a positive impact on this genus, which is not surprising given its known diet flexibility and adaptability to urban habitats (Galetti and Pedroni 1994; Fragaszy et al. 2004). The hotspots for *Cebus* are low, flat areas in São Paulo and Espírito Santo, as well as semideciduous forests in São Paulo and Minas Gerais (Figure 3-4).

Densities for titi monkeys (*Callicebus* spp.) were higher in regions with relatively low mean temperatures, high precipitation, and in fragments embedded in agricultural zones (Table 4-3). The fact that titi monkey densities displayed a positive correlation with agriculture – as opposed to howlers – is interesting and exemplifies the importance of incorporating the landscape context on habitat suitability analyses. Although the mechanism driving these differences is not being examined here, it could be related to hunting pressure. Howlers forage in medium to large groups, and are diurnal, extremely conspicuous species. On the other hand, titi monkeys live in pairs and are canopy foragers, thus less likely to be spotted by poachers. The hotspots for *Callicebus* are the Serra do Mar and Paranapiacaba hill chains in São Paulo, as well as central Minas Gerais (Figure 4-5).

Callithrix displays a preference for locations with intermediate values of climatic variables and income (Table 4-3). The highest estimated density values are associated with ranges of temperature and precipitation that compare favorably with studies done using presence-absence data for this genus (Grelle and Cerqueira 2006). As for the relationship between marmoset density and median income, it is possible that areas with low income have higher hunting pressure, whereas areas with high income also tend to be urbanized. In any case, social indicators proved to be better predictors of marmoset density than land use data. The predicted hotspots for *Callithrix* are the forests in Espírito Santo (Figure 4-6).

Overall, our analyses predict that semideciduous forests in Minas Gerais and São Paulo state have a large potential to support primate populations, despite the fact that most large forest tracts are located along large forest tracts in coastal São Paulo.

Areas in Need of Future Research

Estimates of population sizes derived from the literature suggest that less than half of the study sites in the Brazilian southeast hold viable populations of the five genera studied here (Table 4-1). We assume 500 individuals is the minimal viable population size (Franklin 1980), although some authors consider it an underestimate (Reed et al. 2003). On one hand, it is not known whether small fragments in urban or agricultural zones can support primate populations in the long term (Bernardo and Galetti, 2004). On the other hand, studies still need to show the extent to which primate densities in larger forest tracts reflect their carrying capacity versus their accessibility to poachers. In this scenario, more synthetic studies are needed in order to quantify the relative effects of forest quality and landscape context on primate densities. Here are a few questions that deserve attention:

(i) Are lower densities in large fragments a real pattern? If primates adjust their home ranges in response to fragment size and groups become more mobile in larger fragments, a researcher is more likely to observe individuals in a small fragment than in a large one, even if both areas have similar densities. Perhaps in order to compare density estimates across fragments, sampling effort should be scaled according to species' home range.

(ii) Are populations in small fragments viable? Although genera such as *Alouatta* and *Cebus* have proven very adaptable to live in urban and small forest fragments, it still remains to be seen whether these populations can overcome the possible effects of inbreeding and disease.

(iii) In the present study, we found that variables such as land use and social indicators can serve as surrogates for anthropogenic impact. However, we are presently unable to tease apart the effects of hunting pressure and habitat disturbance. A wealth of socio-economic data is published by IBGE, the Brazilian Institute for Geography and Statistics (www.ibge.gov). If direct estimates of hunting pressure are made available, it would be possible to select the variables that more strongly correlate with hunting pressure.

(iv) Estimates of habitat suitability are highly dependent on the extent of the study area and on the resolution used to collect the data. It is possible that a completely different set of factors will correlate with fine-scale variation in primate densities. For this reason it would be interesting to focus on large conservation units and study within-park variation in primate density.

(v) Finally, primate population studies are not yet available for states such as Rio de Janeiro, Parana, and Bahia. These three states still have large protected parks (e.g., Iguassu, Itatiaia, and Bocaina National Parks) that may hold large primate populations.

ACKNOWLEDGEMENTS

The program BIOTA Fapesp (2001/14463-5) funded the Laboratório de Biologia da Conservação (throught a grant for Mauro Galetti) and the census in the protected areas in Sao Paulo State. MG receives a research fellowship from CNPq. The Teresa Lozano Long Institute of Latin American Studies (LILAS) at Austin, TX for promoting the

exchange program between MG and Timothy H. Keitt. Dr. C. Joly and F. Kronka kindly provided the digital map of vegetation types for Sao Paulo State. S.K. Gobbo, R.M. Marques, C. Steffler, P. Rubim, and R. Nobre provided unpublished data from their study areas.

LITERATURE CITED

Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are these general patterns? Journal of Ecology 84, 597-608.

Alves ACR et al. (2006) Two new species of *Brachycephalus* (Anura: Brachycephalidae) from the Atlantic forest in Parana state, southern Brazil. Herpetologica 62, 221-233.

Berk RA (2006) An introduction to ensemble methods. Sociological Methods and Research 34, 263-295.

Bernardo CS, Galetti M (2004) Densidade e tamanho populacional de primatas em um fragmento florestal no sudeste do Brasil. Revista Brasileira de Zoologia 21, 827-832.

BIOTA (2006) Atlas Sinbiota: http://sinbiota.cria.org.br/index.

Bovendorp RS, Galetti M (2007) Density and population size of mammals introduced on a land-bridge island in southeastern Brazil. Biological Invasions 9, 353-357.

Brashares JS, et al. (2001) Human demography and reserve size predict wildlife extinction in West Africa. Proceedings of the Royal Society of London Series B-Biological Sciences 268, 2473-2478.

Breiman L (2001) Random Forests. Machine Learning 45, 5-32.

Brooks TM, et al. (2000) Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16, 909-923.

Brown JH et al. (1995) Spatial variation in abundance. Ecology 76, 2028-2043.

Buckland ST et al. (2001) Introduction to Distance Sampling. Oxford University Press, Oxford.

Buss G (2001) Estudo da densidade populacional do bugio-ruivo *Alouatta guariba clamitans* (Cabrera, 1940) (Platyrrhini, Atelidae) nas formacoes florestais do

morro do campista, Parque Estadual de Itapua, Viamao, RS. Master Thesis. Universidade Federal do Rio Grande do Sul, Brazil.

Camara IG (2003) Brief history of conservation in the Atlantic forest. In: Gusmao-Camara I, Galindo Leal C (eds.), The Atlantic Forest of South America. Biodiversity Status, Threats, and Outlook. Island Press, Washington, pp. 31-42.

Chiarello AG (1993) Home range of the brown howler monkey, *Alouatta fusca*, in a forest fragment in southeastern Brazil. Folia Primatologica 60, 173-175.

Chiarello AG (2000) Density and population size of mammals in remnants of Brazilian Atlantic Forest. Conservation Biology 14, 1469-1657.

Chiarello AG (2003) Primates of the Brazilian Atlantic forest: the influence of forest fragmentation on survival. In: Marsh K (ed.), Primates in Fragments. Ecology and Conservation. Kluwer Academic, New York, pp. 99-121.

Chiarello AG, Melo FR (2001) Primate population densities and sizes in Atlantic forest remnants of northern Espirito Santo, Brazil. International Journal of Primatology 22, 379-395.

Coley PD (1983) Herbivory and defense characteristics of tree species in a lowland tropical forest. Ecological Monographs 53, 209-233.

Correa HKM, et al. (2000) Between-year differences in the feeding ecology of highland marmosets (*Callithrix aurita* and *Callithrix flaviceps*) in south-eastern Brazil. Journal of Zoology 252, 421-427.

Cosenza BAP, Melo F (1998) Primates of the Serra do Brigadeiro State Park, Minas Gerais, Brazil. Neotropical Primates 6, 18-20.

Cullen Jr., et al. (2001) Ecological consequences of hunting in Atlantic forest patches, Sao Paulo, Brazil. Oryx 35, 137-144.

Danko DM (1992) Digital chart of the world. GeoInfo Systems 29-36.

Dean W (1996) A Ferro e Fogo: A História e a Devastação da Mata Atlântica Brasileira. Companhia das Letras, São Paulo.

DNIT (2007) Atlas das estradas do Brasil. www.dnit.br

Donha CG, Eliasaro S (2006) Two new species of *Parmotrema* (Parmeliaceae, lichenized ascomycota) from Brazil. Mycotaxon 95, 241-245.

Eva HD, et al. (2002) A vegetation map of South America. EUR 20159, European Commission, Joint Research Centre.

Fragaszy DM et al. (2004) Behavioral ecology: how to capuchins make a living? In: Fragaszy DM, Visalberghi E, Fedigan LM (eds.), The Complete Capuchin: the Biology of the Genus Cebus. Cambridge University Press, Cambridge, UK, pp. 36-54.

Franklin, I.R. 1980. Evolutionary change in small populations. In: Soule ME, Wilcox BA (eds.), Conservation Biology: an Evolutionary-Ecological Perspective. Sinauer, Sunderland, MA, pp 135-150.

Galetti M, Pedroni F (1994) Diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in South-east Brazil. Journal of Tropical Ecology 10, 27-39.

Garzon MB, et al. (2006) Predicting habitat suitability with machine learning models: the potential area of *Pinus silvestris* L. in the Iberian peninsula. Ecological Modeling 197, 383-393.

Glander KE (1978) Howler monkey feeding behavior and plant secondary compounds: a study of strategies. In: Montgomery GC (ed.), The Ecology of Arboreal Folivores. Smithsonian Press, Washington.

Godoy R, et al. (2006) Human body-mass index (weight in kg/stature in m(2)) as a useful proxy to assess the relation between income and wildlife consumption in poor rural societies. Biodiversity and Conservation 15, 4495-4506.

Grelle CE, Cerqueira R (2006) Determinantes da distribuicao geografica de *Callithrix flaviceps* (Thomas) (Primates, Callitrichidae). Revista Brasileira de Zoologia 23, 414-420.

Hansen MR, et al. (2003) Vegetation Continuous Fields, MOD44B, 2001 percent tree cover, collection 3. University of Maryland, College Park, Maryland.

Hijmans RJ et al. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965-1978.

Hirota MM (2003) Monitoring the Brazilian Atlantic forest cover. . In: Gusmao-Camara I, Galindo-Leal C (eds.), The Atlantic Forest of South America. Biodiversity Status, Threats, and Outlook. Island Press, Washington, pp. 60-65.

Hirsh A (1995) Censo de *Alouatta fusca* Geoffroy, 1812 (Platyrrhini, Atelidae) e qualidade do habitat em dois remanescentes de Mata Atlantica em Minas Gerais. Master Thesis. Universidade Federal de Minas Gerais.

Hirsh A, et al. (1994) Levantamento de primatas e zoneamento das matas da regiao do Parque Estadual do Ibitipoca, Minas Gerais, Brasil. Neotropical Primates 2, 4-6.

Hirsh A, et al. (2006) Database of Georeferenced Occurrence Localities of Neotropical Primates. Department of Zoology, UFMG, Belo Horizonte.

http://www.icb.ufmg.br/zoo/primatas/home_bdgeoprim.htm

IBGE (1996, 2000) Instituto Brasileiro de Geografia e Estatistica. www.ibge.gov.br

IUCN (2006) Red List of Threatened Species. http://www.iucn.org/themes/ssc/redlist.htm

Lande R, et al. (1987) Effective population size, genetic variation, and their use in population management. In: Soule ME (ed.), Viable Populations in Conservation. Cambridge University Press, New York, pp. 87-123.

Laurance WF, et al. (2005) Impacts of roads and hunting on central African rainforest mammals. Conservation Biology 20, 1251-1261.

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Liaw A, Wiener M (2002) Classification and regression by randomForest. R News 2, 18-22.

Marsden SJ, et al. (2005) How well will Brazil's system of atlantic forest reserves maintain viable bird populations? Biodiversity and Conservation 14, 2835-2853.

Martins MM (2005) Density of primates in four semideciduous forest fragments of Sao Paulo, Brazil. Biodiversity and Conservation 14, 2321, 2329.

Mendes SL (1989) Estudo ecologico de *Alouatta fusca* (Primates: Cebidae) na Estacao Ecologica Caratinga. Revista Nordestina de Biologia 6,71-104.

Milton K (1994) Habitat, diet, and activity patterns of free-ranging woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroy 1806). International Journal of Primatology 5, 491-514.

Michalski F, Peres CA (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape in southern Amazonia. Biological Conservation 124, 383-396.

Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica 32, 793-810.

Pang H, et al. (2006) Pathway analysis using random forests classification and regression. Bioinformatics 22, 2028-2036.

Peres CA (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in Neotropical forests: a case study of howler monkeys (*Alouatta spp.*). Folia Primatologica 68, 199-222.

Pinto LPS, et al. (1993) Habitat, density, and group size of primates in a Brazilian tropical forest. Folia Primatologica 61, 135-143.

Pontes ARM, et al. (2006) A new species of capuchin monkey, *Cebus* (Cebidae, Primates): found at the very brink of extinction in the Pernambuco endemis centre. Zootaxa 1200, 1-12.

Prasad AM, et al. (2006) Newer classification and regression tree techniques: bagging and random forests for ecological prediction. Ecosystems 9, 181-199.

Price EC, Piedade HM (2001) Diet of northern masked titi monkeys (*Callicebus personatus*). Folia Primatologica 72, 335-338.

R Development Core Team (2007) R: a language and environment for statistical computing. http://www.R-project.org

Reed DH, et al. (2003) Empirical estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* 113, 23-34.

Romanini de Oliveira RC, et al. (2003) Estimativa de densidade e tamanho populacional de saua (*Callicebus nigrifons*) em um fragmento de mata em regeneracao, Vicosa, Minas Gerais. Neotropical Primates 11, 91-94.

Rylands AB, Faria DS (1993) Habitats, feeding ecology, and home range size in the genus *Callithrix*. In: Rylands AB (ed.), Marmosets and Tamarins: Systematics, Behavior, and Ecology. Oxford University Press, Oxford, UK, pp. 262-272.

Rylands AB, et al. (1993) Systematics, geographic distribution, and some notes on the conservation status of the Callitrichidae. In: Rylands AB (ed.), Marmosets and Tamarins: Systematics, Behavior, and Ecology. Oxford University Press, Oxford, UK, pp. 11-77.

Shively GE (1997) Poverty, technology, and wildlife hunting in Palawan. Environmental Conservation 24, 57-63.

Siren AH, et al. (2006) The relationship between income and hunting in tropical forests: an economic experiment in the field. Ecology and Society 11, 44.

Strier KB (1991) Diet in a group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*) American Journal of Primatology 23, 113-126.

Strier KB (2000) Population viabilities and conservation implications for muriquis (*Brachyteles arachnoides*) in Brazil's Atlantic forest. Biotropica 32 903-913.

Trevelin LC (2006) Aspectos da ecologia do saua (*Callicebus nigrifons*) no Parque Estadual da Cantareira, SP. Master Thesis. Universidade Estadual Paulista Julio de Mesquita Filho (UNESP).

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3: 385-397.

Appendix

List of studies used in Chapter 3.

Site	Genus	Species	Source	Used in regression?
S. Jose	*Callicebus*	*nifrifons*	1	Y
S. Jose	*Callithrix*	*aurita*	1	Y
S. Jose	*Cebus*	*nigritus*	1	Y
C. Grande	*Callicebus*	*personatus*	2	Y
C. Grande	*Callithrix*	*geoffroyi*	2	Y
C. Grande	*Cebus*	*nigritus*	2	Y
C. Veado	*Callithrix*	*geoffroyi*	2	Y
C. Veado	*Cebus*	*nigritus*	2	Y
Linhares	*Callicebus*	*personatus*	2	Y
Linhares	*Callithrix*	*geoffroyi*	2	Y
Linhares	*Cebus*	*nigritus*	2	Y
Putiri-M7	*Callicebus*	*personatus*	2	Y
Putiri-M7	*Callithrix*	*geoffroyi*	2	Y
Putiri-M7	*Cebus*	*nigritus*	2	Y
Sooretama	*Callicebus*	*personatus*	2	Y
Sooretama	*Callithrix*	*geoffroyi*	2	Y
Sooretama	*Cebus*	*nigritus*	2	Y
Caetetus	*Alouatta*	*fusca*	3	Y
Caetetus	*Cebus*	*nigritus*	3	Y
Caetetus	*Leontopithecus*	*crysopygus*	3	N
F. Rio Claro	*Alouatta*	*clamitans*	3	Y
F. Rio Claro	*Cebus*	*nigritus*	3	Y
F. Rio Claro	*Leontopithecus*	*crysopygus*	3	N
M. Diabo	*Alouatta*	*clamitans*	3	Y
M. Diabo	*Cebus*	*nigritus*	3	Y
M. Diabo	*Leontopithecus*	*crysopygus*	3	N
Mosquito	*Alouatta*	*clamitans*	3	Y
Mosquito	*Cebus*	*nigritus*	3	Y
Mosquito	*Leontopithecus*	*crysopygus*	3	N
Tucano	*Alouatta*	*clamitans*	3	Y
Tucano	*Cebus*	*nigritus*	3	Y
Tucano	*Leontopithecus*	*crysopygus*	3	N
A. Sumida	*Alouatta*	*clamitans*	4	Y
A. Sumida	*Brachyteles*	*arachnoides*	4	Y
A. Sumida	*Cebus*	*nigritus*	4	Y

Monal	*Alouatta*	*clamitans*	4	Y
Monal	*Brachyteles*	*arachnoides*	4	Y
Monal	*Cebus*	*nigritus*	4	Y
Sara	*Alouatta*	*clamitans*	4	Y
Sara	*Brachyteles*	*arachnoides*	4	Y
Sara	*Cebus*	*nigritus*	4	Y
Viraeiro	*Alouatta*	*clamitans*	4	Y
Viraeiro	*Brachyteles*	*arachnoides*	4	Y
Viraeiro	*Cebus*	*nigritus*	4	Y
Vicosa	*Callicebus*	*nigrifons*	5	Y
Caratinga	*Brachyteles*	*hypoxanthus*	6	Y
A. Ruschi, S. Lourenco, S. Lucia	*Alouatta*	*clamitans*	7	Y
A. Ruschi, S. Lourenco, S. Lucia	*Brachyteles*	*hypoxanthus*	7	Y
A. Ruschi, S. Lourenco, S. Lucia	*Callicebus*	*personatus*	7	Y
A. Ruschi, S. Lourenco, S. Lucia	*Callithrix*	*flaviceps*	7	Y
A. Ruschi, S. Lourenco, S. Lucia	*Cebus*	*nigritus*	7	Y
F. Neblina	*Alouatta*	*clamitans*	8	Y
F. Neblina	*Brachyteles*	*arachnoides*	8	Y
F. Neblina	*Callicebus*	*personatus*	8	Y
F. Neblina	*Callithrix*	*aurita*	8	Y
F. Neblina	*Cebus*	*nigritus*	8	Y
Linhares	*Alouatta*	*clamitans*	9	Y
Putiri-M7	*Alouatta*	*clamitans*	9	Y
Carlos Botelho	*Alouatta*	*clamitans*	10	Y
Carlos Botelho	*Brachyteles*	*arachnoides*	10	Y
Carlos Botelho	*Cebus*	*nigritus*	10	Y
Cardoso	*Alouatta*	*clamitans*	10	Y
Ilhabela	*Cebus*	*nigritus*	10	Y
Jureia	*Alouatta*	*clamitans*	10	Y
Jureia	*Brachyteles*	*arachnoides*	10	Y
Jureia	*Cebus*	*nigritus*	10	Y
Jurupara	*Alouatta*	*clamitans*	10	Y
Jurupara	*Cebus*	*nigritus*	10	Y
Picinguaba	*Alouatta*	*clamitans*	10	Y
Picinguaba	*Callithrix*	*aurita*	10	Y
Picinguaba	*Cebus*	*nigritus*	10	Y
S. Virginia-Cunha	*Alouatta*	*clamitans*	10	Y
S. Virginia-Cunha	*Brachyteles*	*arachnoides*	10	Y

S. Virginia-Cunha	*Callithrix*	*aurita*	10	Y
S. Virginia-Cunha	*Cebus*	*nigritus*	10	Y
R. doce	*Alouatta*	*clamitans*	11	Y
Cantareira	*Callicebus*	*nigrifons*	12	Y
Itapua	*Alouatta*	*clamitans*	13	N
S. Genebra	*Alouatta*	*clamitans*	14	N
A. Ruschi, S. Lourenco, S. Lucia	*Alouatta*	*clamitans*	15	N
A. Ruschi, S. Lourenco, S. Lucia	*Brachyteles*	*arachnoides*	15	N
A. Ruschi, S. Lourenco, S. Lucia	*Callicebus*	*personatus*	15	N
A. Ruschi, S. Lourenco, S. Lucia	*Callithrix*	*flaviceps*	15	N
A. Ruschi, S. Lourenco, S. Lucia	*Cebus*	*nigritus*	15	N
Ibitipoca	*Alouatta*	*clamitans*	16	N
Ibitipoca	*Callicebus*	*personatus*	16	N
Ibitipoca	*Callithrix*	*penicillata*	16	N
Anchieta	*Callithrix*	*penicillata*	17	N
Anchieta	*Cebus*	*nigritus*	17	N

Sources: (1) Sao Bernardo and Galetti 2004; (2) Chiarello 2000; (3) Cullen et al. 2001; (4) Martins 2005; (5) Romanini de Oliveira et al. 2003; (6) Strier et al. 2000; (7) Chiarello 2003; (8) Consenza and Melo 1998; (9) Chiarello and Melo 2001; (10) Galetti et al., unpublished data; (11) Hirsh 1995; (12) Trevelin 2006; (13) Buss 2001; (14) Chiarello 1993; (15) Pinto et al. 1994; (16) Hirsh et al. 1994; (17) Bovendorp and Galetti 2007.

Bibliography

Addicott JF et al. (1987) Ecological neighborhoods – scaling environmental patterns. Oikos 49: 340-346.

Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are these general patterns? Journal of Ecology 84, 597-608.

Aldridge HDJN, Rautenbach IL (1987) Morphology, echolocation, and resource partioning in insectivorous bats. Journal of Animal Ecology 56: 763-778.

Alves ACR et al. (2006) Two new species of *Brachycephalus* (Anura: Brachycephalidae) from the Atlantic forest in Parana state, southern Brazil. Herpetologica 62, 221-233.

Belisle M (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. Ecology 86: 1988-1995.

Berk RA (2006) An introduction to ensemble methods. Sociological Methods and Research 34, 263-295.

Bernard E (2001) Vertical stratification of bat communities in primary forests of Central amazon, Brazil. Journal of Tropical Ecology 17: 115-116.

Bernard E, Fenton MB (2003) Bat mobility and roosts in a fragmented landscape in central Amazonia, Brazil. Biotropica 35: 262-277.

Bernardo CS, Galetti M (2004) Densidade e tamanho populacional de primatas em um fragmento florestal no sudeste do Brasil. Revista Brasileira de Zoologia 21, 827-832.

Bestelmeyer BT, Wiens JA (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentinian Chaco. Ecological Applications 6: 1225-1240.

Betts MG et al. (2006) Independent effects of fragmentation on forest songbirds: an organism-based approach. Ecological Applications 16: 1076-1089.

BIOTA (2006) Atlas Sinbiota: http://sinbiota.cria.org.br/index.

Bodin O, et al. (2005) The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. Ecological Applications 16: 440-451.

Boitani L, et al. (2007) Ecological networks as conceptual frameworks or operational tools in conservation. Conservation Biology 21: 1414-1422.

Bonaccorso F (1979) Foraging and reproductive ecology in a Panamanian bat community. Bulletin of Florida State Museum of Biological Sciences 24: 359-408.

Bovendorp RS, Galetti M (2007) Density and population size of mammals introduced on a land-bridge island in southeastern Brazil. Biological Invasions 9, 353-357.

Brashares JS, et al. (2001) Human demography and reserve size predict wildlife extinction in West Africa. Proceedings of the Royal Society of London Series B-Biological Sciences 268, 2473-2478.

Breiman L (2001) Random Forests. Machine Learning 45, 5-32.

Brooks TM, et al. (2000) Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16, 909-923.

Brown JH et al. (1995) Spatial variation in abundance. Ecology 76, 2028-2043.

Buckland ST et al. (2001) Introduction to Distance Sampling. Oxford University Press, Oxford.

Burel F (1996) Hedgerows and their role in agricultural landscapes. Reviews in Plant Sciences 15: 169-190.

Buss G (2001) Estudo da densidade populacional do bugio-ruivo *Alouatta guariba clamitans* (Cabrera, 1940) (Platyrrhini, Atelidae) nas formacoes florestais do morro do campista, Parque Estadual de Itapua, Viamao, RS. Master Thesis. Universidade Federal do Rio Grande do Sul, Brazil.

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and Environment 2: 529-536.

Camara IG (2003) Brief history of conservation in the Atlantic forest. In: Gusmao-Camara I, Galindo Leal C (eds.), The Atlantic Forest of South America. Biodiversity Status, Threats, and Outlook. Island Press, Washington, pp. 31-42.

Chardon JP, et al. (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (*Parge aegeria* L.). Landscape Ecology 18: 561-573.

Chetkiewicz CLB, et al. (2006) Corridors for conservation: integrating pattern and process. Annual Review of Ecology and Systematics 37: 317-342.

Chiarello AG (1993) Home range of the brown howler monkey, *Alouatta fusca*, in a forest fragment in southeastern Brazil. Folia Primatologica 60, 173-175.

Chiarello AG (2000) Density and population size of mammals in remnants of Brazilian Atlantic Forest. Conservation Biology 14, 1469-1657.

Chiarello AG (2003) Primates of the Brazilian Atlantic forest: the influence of forest fragmentation on survival. In: Marsh K (ed.), Primates in Fragments. Ecology and Conservation. Kluwer Academic, New York, pp. 99-121.

Chiarello AG, Melo FR (2001) Primate population densities and sizes in Atlantic forest remnants of northern Espirito Santo, Brazil. International Journal of Primatology 22, 379-395.

Clevenger AP, et al. (2001) Drainage culverts as habitat linkages and factors affecting passage by mammals. Journal of Applied Ecology 38: 1340-1349.

Coley PD (1983) Herbivory and defense characteristics of tree species in a lowland tropical forest. Ecological Monographs 53, 209-233.

Cormen TH, et al. (2001) Introduction to Algorithms. MIT Press, Cambridge, Massachusetts.

Correa HKM, et al. (2000) Between-year differences in the feeding ecology of highland marmosets (*Callithrix aurita* and *Callithrix flaviceps*) in south-eastern Brazil. Journal of Zoology 252, 421-427.

Cosenza BAP, Melo F (1998) Primates of the Serra do Brigadeiro State Park, Minas Gerais, Brazil. Neotropical Primates 6, 18-20.

Cosson JF et al. (1999) Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. Journal of Tropical Ecology 15: 515-534.

Cressie NAC (1993) Statistics for Spatial Data. -Wiley.

Cullen Jr., et al. (2001) Ecological consequences of hunting in Atlantic forest patches, Sao Paulo, Brazil. Oryx 35, 137-144.

Danko DM (1992) Digital chart of the world. GeoInfo Systems 29-36.

Dean W (1996) A Ferro e Fogo: A História e a Devastação da Mata Atlântica Brasileira. Companhia das Letras, São Paulo.

DNIT (2007) Atlas das estradas do Brasil. www.dnit.br

Donha CG, Eliasaro S (2006) Two new species of *Parmotrema* (Parmeliaceae, lichenized ascomycota) from Brazil. Mycotaxon 95, 241-245.

Drielsma M et al. (2007) A raster-based technique for analyzing habitat configuration: the cost-benefit approach. Ecological Modeling 202: 324-332.

Driezen K, et al. (2007) Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). Ecological Modelling 209: 314-322.

Emmons LH, Feer, F (1997) Neotropical Forest Mammals. A Field Guide. - University of Chicago Press.

Estrada AJ, Coates-Estrada R (2002) Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biological Conservation 103: 237-245.

Eva HD, et al. (2002) A vegetation map of South America. EUR 20159, European Commission, Joint Research Centre.

Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecological Modelling 160: 115-130.

Faria D (2006) Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. Journal of Tropical Ecology 22: 531-542.

Fragaszy DM et al. (2004) Behavioral ecology: how to capuchins make a living? In: Fragaszy DM, Visalberghi E, Fedigan LM (eds.), The Complete Capuchin: the Biology of the Genus Cebus. Cambridge University Press, Cambridge, UK, pp. 36-54.

Franklin, I.R. 1980. Evolutionary change in small populations. In: Soule ME, Wilcox BA (eds.), Conservation Biology: an Evolutionary-Ecological Perspective. Sinauer, Sunderland, MA, pp 135-150.

Galetti M, Pedroni F (1994) Diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in South-east Brazil. Journal of Tropical Ecology 10, 27-39.

Galindo-Gonzalez J et al. (2000) Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology 14: 1693-1703.

Garzon MB, et al. (2006) Predicting habitat suitability with machine learning models: the potential area of *Pinus silvestris* L. in the Iberian peninsula. Ecological Modeling 197, 383-393.

Glander KE (1978) Howler monkey feeding behavior and plant secondary compounds: a study of strategies. In: Montgomery GC (ed.), The Ecology of Arboreal Folivores. Smithsonian Press, Washington.

Godoy R, et al. (2006) Human body-mass index (weight in kg/stature in m(2)) as a useful proxy to assess the relation between income and wildlife consumption in poor rural societies. Biodiversity and Conservation 15, 4495-4506.

Goodwin BJ (2003). Is landscape connectivity a dependent of independent variable? Landscape ecology 18: 687-699.

Gorresen PM et al. (2005) Multivariate analysis of scale-dependent associations between bats and landscape structure. Ecological Applications 15: 2126-2136.

Grelle CE, Cerqueira R (2006) Determinantes da distribuicao geografica de *Callithrix flaviceps* (Thomas) (Primates, Callitrichidae). Revista Brasileira de Zoologia 23, 414-420.

Hansen MR, et al. (2003) Vegetation Continuous Fields, MOD44B, 2001 percent tree cover, collection 3. University of Maryland, College Park, Maryland.

Hanski I (1994) A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151-162.

Heithaus ER, Fleming TH (1978) Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomatidae). Ecological Monographs 48: 127-143.

Henry M et al. (2007) Abundance may be a misleading indicator of fragmentation-sensitivity: the case of fig-eating bats. Biological Conservation 139: 462-467.

Hess GR, Fischer RA (2001) Communicating clearly about corridors. Landscape and Urban Planning 55: 195-208.

Hijmans RJ et al. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965-1978.

Hirota MM (2003) Monitoring the Brazilian Atlantic forest cover. . In: Gusmao-Camara I, Galindo-Leal C (eds.), The Atlantic Forest of South America. Biodiversity Status, Threats, and Outlook. Island Press, Washington, pp. 60-65.

Hirsh A (1995) Censo de *Alouatta fusca* Geoffroy, 1812 (Platyrrhini, Atelidae) e qualidade do habitat em dois remanescentes de Mata Atlantica em Minas Gerais. Master Thesis. Universidade Federal de Minas Gerais.

Hirsh A, et al. (1994) Levantamento de primatas e zoneamento das matas da regiao do Parque Estadual do Ibitipoca, Minas Gerais, Brasil. Neotropical Primates 2, 4-6.

Hirsh A, et al. (2006) Database of Georeferenced Occurrence Localities of Neotropical Primates. Department of Zoology, UFMG, Belo Horizonte.

Hoctor TS, et al. (2000) Identifying a linked reserve system using a regional landscape approach: the Florida ecological network. Conservation Biology 14: 984-1000.

http://www.icb.ufmg.br/zoo/primatas/home_bdgeoprim.htm

IBGE (1991) Census of Brazilian municipalities. Available from http:// www.ibge.gov.br

IBGE (1996, 2000) Instituto Brasileiro de Geografia e Estatistica. www.ibge.gov.br

IUCN (2006) Red List of Threatened Species. http://www.iucn.org/themes/ssc/redlist.htm

Kalko EK et al. (1996) Organization, diversity, and long-term dynamics of a Neotropical bat community. In: Cody M, Smallwood J (eds.), Long-Term Studies of Vertebrate Communities. Academic Press, pp. 503-548.

Keitt TH, et al. (1997) Detecting critical scales in fragmented landscapes. Conservation Ecology [online] 1: 4. Available from the internet: URL: http://www.consecol.org/vol1/iss1/art4

Keitt TH, Urban DL (2005) Scale-specific inference using wavelets. Ecology 86: 2497-2504.

Kremen C et al. (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters 7: 1109-1119.

Lande R, et al. (1987) Effective population size, genetic variation, and their use in population management. In: Soule ME (ed.), Viable Populations in Conservation. Cambridge University Press, New York, pp. 87-123.

Larkin JL, et al. (2004) Landscape linkage and conservation planning for the black bear in west-central Florida. Animal Conservation 7: 23-34.

Laurance WF, et al. (2002) Ecosystem decay of forest fragments: a 22-year investigation. Conservation Biology 16: 605-618.

Laurance WF, et al. (2005) Impacts of roads and hunting on central African rainforest mammals. Conservation Biology 20, 1251-1261.

Lees AC, Peres CA (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conservation Biology *in press*.

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Liaw A, Wiener M (2002) Classification and regression by randomForest. R News 2, 18-22.

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Mallat, SG (1989) A theory for multiresolution signal decomposition: the wavelet representation. IEEE Transactions on Pattern Analysis and Machine Intelligence 11: 674-693.

Manning AD, et al. (2006) Scattered trees as keystone structures – implications for conservation. Biological Conservation 132: 311-321.

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

Marinho-Filho JS (1991) The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. Journal of Tropical Ecology 7: 59-67.

Marsden SJ, et al. (2005) How well will Brazil's system of atlantic forest reserves maintain viable bird populations? Biodiversity and Conservation 14, 2835-2853.

Martins MM (2005) Density of primates in four semideciduous forest fragments of Sao Paulo, Brazil. Biodiversity and Conservation 14, 2321, 2329.

Mas AH, Dietsch TV (2003) An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. Ecological Applications 13: 1491-1501.

McNab B (1963) Bioenergetics and the determination of home range size. American Naturalist 97: 133-140.

Mendes SL (1989) Estudo ecologico de *Alouatta fusca* (Primates: Cebidae) na Estacao Ecologica Caratinga. Revista Nordestina de Biologia 6,71-104.

Michalski F, Peres CA (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape in southern Amazonia. Biological Conservation 124, 383-396.

Milton K (1994) Habitat, diet, and activity patterns of free-ranging woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroy 1806). International Journal of Primatology 5, 491-514.

Minns CK (1995) Allometry of home-range size in lake and river fishes. Canadian Journal of Fisheries and Aquatic Sciences. 52: 1499-1508.

Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13: 11-21.

Montiel S, et al. (2005) Bat assemblages in a naturally fragmented ecosystem in the Yucatan peninsula, Mexico: species richness, diversity and spatio-temporal dynamics. Journal of Tropical Ecology 22: 267-276.

Morellato LPC, Haddad CFB (2000) Introduction: the Brazilian Atlantic forest. Biotropica 32: 786-792.

Morrison DW (1978a) Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. Ecology 59: 716-723.

Morrison DW (1978b) Influence of habitat on the foraging distances of the fruit bat, *Artibeus jamaicensis.* Journal of Mammalogy 59: 622-624.

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia: Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B 316: 335-427.

Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica 32, 793-810.

Pang H, et al. (2006) Pathway analysis using random forests classification and regression. Bioinformatics 22, 2028-2036.

Peres CA (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in Neotropical forests: a case study of howler monkeys (*Alouatta spp.*). Folia Primatologica 68, 199-222.

Perfecto I, et al. (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation 12: 1239-1252.

Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conservation Biology 16: 174-182.

Pineda E et al. (2005) Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. Conservation Biology 19: 400-410.

Pinto LPS, et al. (1993) Habitat, density, and group size of primates in a Brazilian tropical forest. Folia Primatologica 61, 135-143.

Pontes ARM, et al. (2006) A new species of capuchin monkey, *Cebus* (Cebidae, Primates): found at the very brink of extinction in the Pernambuco endemis centre. Zootaxa 1200, 1-12.

Prasad AM, et al. (2006) Newer classification and regression tree techniques: bagging and random forests for ecological prediction. Ecosystems 9, 181-199.

Price EC, Piedade HM (2001) Diet of northern masked titi monkeys (*Callicebus personatus*). Folia Primatologica 72, 335-338.

R Development Core Team (2007) R: a language and environment for statistical computing. http://www.R-project.org

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-projects.org.

Reed DH, et al. (2003) Empirical estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* 113, 23-34.

Reitsma R, et al. (2001) The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. Agroforestry Systems 53: 185-193.

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158: 87-99.

Romanini de Oliveira RC, et al. (2003) Estimativa de densidade e tamanho populacional de saua (*Callicebus nigrifons*) em um fragmento de mata em regeneracao, Vicosa, Minas Gerais. Neotropical Primates 11, 91-94.

Rylands AB, et al. (1993) Systematics, geographic distribution, and some notes on the conservation status of the Callitrichidae. In: Rylands AB (ed.), Marmosets and Tamarins: Systematics, Behavior, and Ecology. Oxford University Press, Oxford, UK, pp. 11-77.

Rylands AB, Faria DS (1993) Habitats, feeding ecology, and home range size in the genus *Callithrix*. In: Rylands AB (ed.), Marmosets and Tamarins: Systematics, Behavior, and Ecology. Oxford University Press, Oxford, UK, pp. 262-272.

Sanderson EW et al. (2002) The human footprint and the last of the wild. Bioscience 52: 891-904.

Schadt S, et al. (2002) Rule-based assessment of suitable habitat and patch connectivity for Eurasian Lynx in Germany. Ecological Applications 12: 1469-1483.

Scheiner SM et al. (2000) Species richness, species-area curves and Simpson's paradox. Evolutionary Ecology Research 2: 791-802.

Schulze MD et al. (2000). A comparison of the phyllostomid bat assemblages in undisturbed Neotropical forest and in forest fragments in a slash-and-burn farming mosaic in Peten, Guatemala. Biotropica 32: 174-184.

Shively GE (1997) Poverty, technology, and wildlife hunting in Palawan. Environmental Conservation 24, 57-63.

Simmons NB, Voss RS (1998). The mammals of Paracou, French Guiana: a Neotropical rainforest fauna. Part I. Bats. Bulletin of the American Museum of Natural History 237: 1-219.

Siren AH, et al. (2006) The relationship between income and hunting in tropical forests: an economic experiment in the field. Ecology and Society 11, 44.

Soto M, Gama L (1997) Climas. In: González-Soriano E, et al. (eds.), Historia Natural de Los Tuxtlas. Universidad Nacional Autonoma de Mexico, Mexico, pp. 7-23.

Stevens VM, et al. (2006) Gene flow and functional connectivity in the Natterjack toad (*Bufo calamita*). Molecular Ecology 15: 2333-2344.

Stockwell EF (2001) Morphology and flight maneuverability in New World leaf-nosed bats (Chiroptera: Phyllostomidae). Journal of Zoology 254: 505-514.

Strier KB (1991) Diet in a group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*) American Journal of Primatology 23, 113-126.

Strier KB (2000) Population viabilities and conservation implications for muriquis (*Brachyteles arachnoides*) in Brazil's Atlantic forest. Biotropica 32 903-913.

Sutcliffe OL, et al. (2003) Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landscape and Urban Planning 63: 15-31.

Swihart RK et al. (1998) Relating body size to the rate of home range use in mammals. Ecology 69: 393-399.

Tewksbury JJ et al. (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. Proceedings of the National Academy of Sciences 99: 12923-12926.

Trevelin LC (2006) Aspectos da ecologia do saua (*Callicebus nigrifons*) no Parque Estadual da Cantareira, SP. Master Thesis. Universidade Estadual Paulista Julio de Mesquita Filho (UNESP).

Tscharntke T, et al. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8: 857-874.

Turchin P (1998) Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Sinauer Associates, Massachusetts, USA.

Urban DL, Keitt TH (2001) Landscape connectedness: a graph theoretic perspective. Ecology 82: 1205-1218.

Vandermeer J, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. American Naturalist 158: 211-220.

Verbeylen G et al. (2003) Does matrix resistance influence Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? Landscape Ecology 18: 791-805.

Wiens JA (1976) Population responses to patchy environments. Annual Review of Ecology and Systematics 7: 81-210.

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3: 385-397.

Wiens JA et al. (1993) Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

Winfree R et al. (2005) Testing simple indices of habitat proximity. American Naturalist 165: 707-717.

With KA et al. (1999) Movement responses to patch structure in experimental fractal landscapes. Ecology 80: 1340-1353.

Vita

Naiara Sardinha-Pinto was born in Belo Horizonte, Brazil, on October 20, 1979, the daughter of Anelina Costa Souza and Franklin Tatuhy Sardinha-Pinto. After completing work at Pitágoras High School, Belo Horizonte, in 1996, she attended the State University of Campinas (UNICAMP). She received a Bachelor of Science degree in Biology in February 2001. Afterwards, she worked as a research assistant at UNICAMP's Genetics Institute. In 2002, she entered the Graduate School of The University of Texas.

Permanent address: Rua Cuiabá 1097, Prado, Belo Horizonte, MG, 30410-140, Brazil.

This dissertation was typed by the author.